BEHAVIORAL AND DEMOGRAPHIC RESPONSES TO HABITAT CHANGE BY THE TANA RIVER CRESTED MANGABEY (*Cercocebus galeritus galeritus*)

By

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To Ratilli Kawa

and the women of rural East Africa

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TABLE OF CONTENTS

ACKNOWLEDGMENTS iii

LIST OF TABLES x

LIST OF FIGURES xiv

ABSTRACT xx

CHAPTER ONE INTRODUCTION 1

CHAPTER TWO ABUNDANCE AND DISTRIBUTION OF FRUIT RESOURCES IN THREE TANA RIVERINE FORESTS 12
Introduction 12
Methods 14
Study Sites 14
Abundance and Distribution of Resources . . . 17
Environmental Correlates with Flowering and Fruiting 24
Comparisons with 1973-74 25
Results 26
Abundance and Spatial Distribution of Resources 26
Temporal Distribution of Resources 27
Environmental Correlates with Flowering and Fruiting 60
Comparisons with 1973-74 72
Discussion 73

CHAPTER THREE ACTIVITY PATTERNS AND DIET OF THE TANA RIVER CRESTED MANGABEY: EFFECTS OF SEASONAL AND LONG-TERM HABITAT CHANGE 79
Introduction 79
Methods 82
Data Collection 82
Data Analysis 85
Results 86
Variation in Activities 1988-89 86
Comparison with 1973-74 Activity Budgets . . 101
Diet 111
Discussion 124

CHAPTER FOUR COMPETING USES OF A FOREST PALM, PHOENIX RECLINATA N. J. JACQUIN, BY HUMANS AND TANA RIVER CRESTED MANGABEYS 136
Introduction 136
Methods 138
Study Species 138
Data Collection 139
Results 141
Discussion 149

CHAPTER FIVE TANA RIVER CRESTED MANGABEY HOME RANGE AND SPATIAL DEFENSE: EFFECTS OF FRUIT ABUNDANCE AND DISTRIBUTION 153
Introduction 153
Methods 155
Data Collection 155
Data Analysis 157
Results 160
Use of Space 160
Movements 179
Intergroup Behavior 186
Discussion 205

CHAPTER SIX POPULATION VIABILITY OF THE TANA RIVER CRESTED MANGABEY 214
Introduction 214
Methods 216
Mangabey Data Set 216
Population Genetics Model 219
Demographic Extinction Model 226
Results 227
Estimates of Ne 227
Population Subdivision 224
Demographic Extinction Model 236
Discussion 242
Effective Population Size 242
Demographic Extinction Model 246

CHAPTER SEVEN CONCLUSION 249

APPENDIX A ESTIMATING TREE CANOPY SURFACE AREA AND VOLUME 255

APPENDIX B NUMBER OF FEEDING RECORDS AND PERCENT OF TOTAL RECORDS BY PLANT TAXON AND MANGABEY GROUP 258

REFERENCES 261

BIOGRAPHICAL SKETCH 277

LIST OF TABLES

Table 2.1. Composition of monthly phenology sample by species for Mchelelo, Nkano and Mnazini forests. . 20

Table 2.2. Density of reproductive trees and lianas enumerated in 16.32 ha of Mchelelo forest and 13.45 ha in Nkano forest, and the degree of clumping of each species using Morisita's index (I_δ). If I_δ is significantly greater or less than unity using the F-test, the species is considered clumped or evenly distributed in space, respectively. If I_δ is not significantly different from unity than the species is considered randomly distributed. 27

Table 2.3. Estimated canopy surface area (S), canopy volume (V), mean fruit production (FN) and mean fruit weight (FW) for 16 species. Species are categorized into 4 groups: those that bear their fruits on the canopy surface (C) or along the branches of the tree (R), lianas (L) and palms (P) 54

Table 2.4. Spearman's rank correlation coefficients for mean monthly environmental variables and mean monthly fruiting scores for Mchelelo forest. MINTEMP=minimum monthly temperature; RAIN=total monthly rainfall (mm); RAINLAG1, RAINLAG2 AND RAINLAG3=monthly rainfall lagged by 1,2, and 3 months, respectively; RAINADV=previous months' rainfall; FLOW=mean monthly river flow (mcm); FLOWLAG1, FLOWLAG2, FLOWLAG3=mean monthly river flow lagged by 1,2 and 3 months, respectively; FLOWADV=previous months' mean river flow. 68

Table 2.5. Spearman's rank correlation coefficients for mean monthly environmental variables and mean monthly fruiting scores for Nkano forest. Variables defined in Table 2.4 69

Table 2.6. Spearman's rank correlation coefficients for mean monthly environmental variables and mean monthly fruiting scores for Mnazini forest. Variables defined in Table 2.4 70

Table 2.7. Spearman's rank correlation coefficients for mean monthly environmental variables and mean monthly fruiting scores for all forests combined. Variables defined in Table 2.4 71

Table 3.1. Mean percent time spent in each activity by each month by mangabeys in the 1988-89 N. Mchelelo, S. Mchelelo, and Nkano study groups. Standard errors are in parentheses. See text for definition of activities 90

Table 3.2. MANOVA results for group membership, season, and time-of-day differences in 1988-89 mangabey activity budgets 91

Table 3.3. ANOVA results for group membership, season, and time-of-day differences in 7 behaviors. Significance values are calculated from Type III partial sums of squares. 92

Table 3.4. ANOVA results for study (Homewood's 1973-74 study and the present 1988-89 study) and age differences in 3 measures of mother/infant association: a) amount of time infant is on its' mother, b) amount of time infant has mother as nearest neighbor and c) amount of time infant is separate from mother. Data were nested by infants within studies. 110

Table 3.5. Rank order of the five most common plant species eaten and the percentage of the total feeding records for identified plants (N) by group and month. Complete scientific names of plant species listed in Appendix B 113

Table 3.6. Percentage of diet items eaten by month and group. Unidentified items are not included. . . . 115

Table 3.7. Frequency of plant parts eaten for common diet species of the 3 study groups. 117

Table 4.1. Human uses of P. reclinata grouped into 6 broad categories. Plant parts utilized and harvesting methods employed are outlined. 142

Table 5.1. Mean diversity of quadrat use (H'), mean number of unique quadrats entered, mean distances travelled, mean half-hour step distances, mean turning angles, and mean number of path crossings by month for the 3 study groups. 178

Table 5.2. Spearman's Rank correlation coefficients (r_s) between frequency of quadrat use by mangabeys and frequency of occurrence of top 5 plant diet species each month for the North Mchelelo, South Mchelelo, and Nkano groups. (-) indicates that ranging data or plant frequency data were not available for all top 5 diet species that month. . 180

Table 5.3. ANOVA results for effect of South Mchelelo group presence and month on distance traveled and measures of travel pattern and use of space by North Mchelelo group. F-statistics are calculated from Type III partial sums of squares 190

Table 5.4. Number of adult male long-calls by study group and month. North refers to long-calls given by the North Mchelelo group males. South M refers to long-calls given by the South Mchelelo group males while present in Mchelelo forest and South C refers to long-calls given by the South Mchelelo group males while in the neighboring Congolani forest. Alien refers to long-calls given by males of a second, unhabituated group in Nkano forest, and Unk represents long-calls of unidentified males in the Nkano forest. 192

Table 5.5. Intergroup behavior categories and measures of proximity and fighting by month. F, M, and A designate fights, merge, and avoid months, respectively. N includes all 12-hr observation days and days for which only presence or absence of South group was determined 194

Table 6.1. Minimum and maximum numbers of mangabey groups censused in forests on the east and west banks of the lower Tana River in 1988-89 and 1973-74. Forests not censused indicated with (-); those no longer standing indicated with (x). Data from 1973-74 taken from Homewood (1976) and Marsh (1976, 1978). 217

Table 6.2. Age-sex composition of 7 mangabey groups with comparative means from 1973-74 (Homewood 1976). AM = adult male (>4-5 yr); SubM = subadult male (3-5 yr); AF = adult female (>4 yr); SubF = subadult female (2.5-3 yr); JM = juvenile male (8 mon-3 yr); JF = juvenile female (8 mon-2.5 yr); IM and IF = infant male and infant female, respectively ($\leq$ 7 mon) 218

Table 6.3. Reproductive parameters for male and female mangabeys. 220

Table 6.4. Minimum and maximum parameter values and estimates of effective population size. N = census number of males or females; K = estimate of lifetime reproductive success of males or females; K_v = variance in lifetime reproductive success; and N_e = effective population size. Subscripts denote parameters for males vs females. 229

Table 6.5. Parameter values and estimates of the genetic fixation index, F_n, for forests on east and west banks and for west bank and east bank subpopulations. East vs west bank figures are calculated for group migration from one bank to the other for two estimates of high flood frequency 235

LIST OF FIGURES

Figure 1.1. Adult male Tana River crested mangabey, Cercocebus galeritus galeritus, seated in a Hypheane compressa palm 3

Figure 1.2. Map of Kenya and location of the Tana River National Primate Reserve (TRNPR; map modified from Hughes 1985) 8

Figure 2.1. Map of the study area showing the Mchelelo, Mnazini, and Nkano forests within the Tana River National Primate Reserve 16

Figure 2.2. Number of individuals/0.25 ha of 4 common species within Mchelelo forest showing clumped spatial distributions a) Hyphaene compressa; b)Alangium salviifolium; c)Phoenix reclinata; d) Oncoba spinosa 30

Figure 2.3. Number of individuals/0.25 ha of 4 common species within Nkano forest showing clumped spatial distributions. a) Ficus sycomorus; b) Alangium salviifolium; c) Phoenix reclinata; d) Pachystela msolo 32

Figure 2.4. Examples of randomly distributed Ficus spp. a) Ficus natalensis in Mchelelo forest; b) Ficus sycomorus in Mchelelo forest; c) Ficus natalensis in Nkano forest 34

Figure 2.5. Mean flower scores averaged over all species by month. a) Mchelelo forest; b) Nkano forest; c) Mnazini forest 36

Figure 2.6. Mean fruiting scores averaged over all species by month. a) Mchelelo forest; b) Nkano forest; c) Mnazini forest 38

Figure 2.7. Mean monthly fruit scores from Mchelelo and Mnazini forests for Mimusops fruticosa and Acacia robusta, seasonally fruiting species with 1 peak in fruiting per year. a) Mimusops fruiticosa in Mchelelo forest; b) Acacia robusta in Mchelelo forest; c) Mimusops fruticosa in Mnazini forest; d) Acacia robusta in Mnazini forest 41

Figure 2.8. Mean monthly fruit scores from Mchelelo and Mnazini forests for Garcinia livingstonei and Sorindeia madagascariensis, seasonally fruiting species with 2 fruiting peaks per year. a) Garcinia livingstonei in Mchelelo forest; b) Sorindeia madagascariensis in Mchelelo forest; c) Garcinia livingstonei in Mnazini forest; d) Sorindeia madagascariensis in Mnazini forest 43

Figure 2.9. Mean monthly fruit scores for Phoenix reclinata. a) Mchelelo forest; b) Nkano forest; c) Mnazini forest 45

Figure 2.10. Mean monthly fruit scores for Diospyros mespiliformes. a) Mchelelo forest; b) Nkano forest; c) Mnazini forest 47

Figure 2.11. Mean monthly fruit scores for 3 species showing patterns of continuous fruit production. a) continuous fruiting due to asynchrony among individuals of the species (Ficus natalensis); b) continuous fruiting due to retention of fruits over time (Hyphaene compressa); c) continuous fruiting due to rapid turnover of fruits (Oncoba spinosa) 49

Figure 2.12. Mean monthly fruit scores for Ficus sycomorus. a) Mchelelo forest; b) Nkano forest; c) Mnazini forest 51

Figure 2.13. Seasonality of mean monthly fruit scores for Saba comorensis in the 3 study forests. a) seasonal fruiting in Mnazini forest; b) seasonal but extended fruiting in Nkano forest; c) continuous fruiting in Mchelelo forest 53

Figure 2.14. Contribution to monthly fruit biomass indices by different species categories. a) Mchelelo forest; b) Nkano forest; c) Mnazini forest 56

Figure 2.15. Contribution of ripe and unripe fruits to monthly fruit biomass index. a) Mchelelo forest; b) Nkano forest; c) Mnazini forest. 59

Figure 2.16. Monthly mean minimum and mean maximum air temperature in degrees centigrade. a) Mchelelo forest; b) Nkano/Mnazini forest areas 62

Figure 2.17. Total monthly rainfall in millimeters. a) Mchelelo forest; b) Nkano/Mnazini forest area . 64

Figure 2.18. Mean monthly river flow for the Tana River Hola Station 66

Figure 3.1. Mean annual percent time spent among 7 behaviors by three 1988-89 mangabey groups and two 1973-74 mangabey groups. a) 1988-89; b) 1973-74 . 89

Figure 3.2. Mean percent time spent in 4 major behaviors (eating, foraging, moving and inactive) by time-of-day and season for the 1988-89 N. Mchelelo group. 96

Figure 3.3. Mean percent time spent in 4 major behaviors (eating, foraging, moving and inactive) by time-of-day and season for the 1988-89 S. Mchelelo group 98

Figure 3.4. Mean percent time spent in 4 major behaviors (eating, foraging, moving and inactive) by time-of-day and season for the 1988-89 Nkano group 100

Figure 3.5. Mean percent time spent in 7 social behaviors by 1973-74 and 1988-89 adult males and females. a) adult males; b) adult females 104

Figure 3.6. Mean percent time spent in 7 social behaviors by three age-sex classes in 1973-74 and 1988-89. a) juvenile males; b) juvenile females; c) male and female infants combined 106

Figure 3.7. Percent time 1988-89 and 1973-74 infants spent in 3 levels of association with their mothers. Asterisks denote months when levels of association were significantly different between the 2 study periods. a) Association A: the amount of time an infant was on its mother; b) Association B: the amount of time an infant had its mother as nearest neighbor; c) Association C: the amount of time infants were separate from their mothers 109

Figure 3.8. Percent composition of diet by item for 1973-74 and 1988-89. a) 1988-89; b) 1973-74 . . . 119

Figure 3.9. Percent ripe and unripe fruit and seed items inthe diet. a) for three 1988-89 mangabey groups; b) for 1973-74 mangabey groups 123

Figure 4.1. The number of harvested and unharvested palms in Nkano and the number of reproductive and nonreproductive palms in Mchelelo by size class. a) harvested and unharvested palms by size class in Nkano; b) reproductive and nonreproductive palms in Mchelelo by size class 145

Figure 4.2. The number of feeding observations on P. reclinata by month and item for mangabeys in the Mchelelo and Nkano forests 148

Figure 5.1. Cumulative frequency of sightings of one or more North Mchelelo group mangabeys versus rank order of 0.25 h quadrats. Quadrats were ranked with respect to the number of sightings occurring in each. The areas accounting for 50 and 100% of all sightings are designated 162

Figure 5.2. Cumulative frequency of sightings of one or more South Mchelelo group mangabeys versus rank order of 0.25 h quadrats. Quadrats were ranked with respect to the number of sightings occurring in each. The areas accounting for 50 and 100% of all sightings are designated 164

Figure 5.3. Cumulative frequency of sightings of one or more Nkano group mangabeys versus rank order of 0.25 ha quadrats. Quadrats were ranked with respect to the number of sightings occurring in each. The areas accounting for 50 and 100% of all sightings are designated 166

Figure 5.4. Taut-string line (shaded with diagonal lines) enclosing all ad libitum sightings of South Mchelelo group when the group ranged outside the Mchelelo forest 168

Figure 5.5. Frequency distributions of intensity of quadrat use. Asterisks indicate the values expected if quadrat occupancy were random (following a Poisson distribution).a) Frequency distribution for N. Mchelelo group; b) Frequency distribution for S. Mchelelo group; c) Frequency distribution for Nkano group 171

Figure 5.6. Occupancy of each 0.25 ha quadrat by North and South Mchelelo groups; percent occupancy is divided into 1 of 5 intensities of use 173

Figure 5.7. Occupancy of each 0.25 ha quadrat by Nkano group; percent occupancy is divided into 1 of 5 intensities of use 175

Figure 5.8. Frequency distributions of half-hour distance steps in intervals of 20 m. Asterisks indicate values expected if distance steps were distributed randomly (following a Poisson distribution). a) Frequency distribution for N. Mchelelo group; b) Frequency distribution for S. Mchelelo group; c) Frequency distribution for Nkano group 182

Figure 5.9. Frequency distributions of half-hour turning angles in 10 degree intervals. a) Frequency distribution for N. Mchelelo group; b) Frequency distribution for S. Mchelelo group; c) Frequency distribution for Nkano group 185

Figure 5.10. Degree of monthly overlap by North Mchelelo group (solid line) and South Mchelelo group (broken line) and the area of overlap in hectares (bars) . 189

Figure 5.11. Daily travel paths by North and South Mchelelo groups during one day of a month of intergroup avoidance. Timing and location of adult male long-calls are plotted for North (ovals) and South (rectangles) groups 196

Figure 5.12. Daily travel paths by North and South Mchelelo groups during one day of a month of intergroup merging. Timing and location of adult male long-calls are plotted for North (ovals) and South (rectangles) groups 198

Figure 5.13. Daily travel paths by North and South Mchelelo groups during one day of a month of intergroup fighting. Timing and location of adult male long-calls are plotted for North (ovals) and South (rectangles) groups 201

Figure 5.14. Location and outcome of 34 fights observed between North and South Mchelelo groups. N and S indicate that North and South group won fights, respectively. D indicates that no clear winner was determined 204

Figure 5.15. Percent time North and South Mchelelo groups spent feeding on foods with different distributions as a function of intergroup behavior. a) Percent time feeding on foods with uniform distributions; b) Percent time feeding on foods with patchy distributions 207

Figure 6.1. Distribution of estimated female lifetime reproductive success. Infant values are rounded to the nearest whole number 231

Figure 6.2. Distribution of male lifetime reproductive success estimated for males with 1, 2 and 3 tenures as a dominant, breeding group male. a) 1973-74 male lifetime reproductive success calculated for 1 male: 9.75 females; b) 1988-89 male lifetime reproductive success calculated for 1 male:5.85 females 233

Figure 6.3. Persistence time in years as a function of population size (N). Dashed lines connect 1973-74 and 1988-89 population sizes to estimated mean persistence times. 238

Figure 6.4. Probability of extinction p(E) within 100, 50, 25, and 10 years (denoted by labeled curves) for populations with mean persistence times (T) of 200 to 2000 years 241

Figure 6.5. Effective population size (N_e) as a function of number of breeders (N_b) and variance of male lifetime reproductive success (V_m) 244

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BEHAVIORAL AND DEMOGRAPHIC RESPONSES TO HABITAT CHANGE BY THE TANA RIVER CRESTED MANGABEY (CERCOCEBUS GALERITUS GALERITUS)

By

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The Tana River crested mangabey (Cercocebus galeritus galeritus) is an endangered primate found only in small forests of the Tana River in Kenya. The mangabey is afforded some protection in the Tana River National Primate Reserve. Since the establishment of the reserve in 1976 the mangabey population has decreased by 45%. The reduction in habitat size and quality is believed to have been a major factor contributing to the population decline. I compare data on mangabey behavior and demography with a study conducted in 1973-74 to investigate the effects of habitat loss and reductions in important diet species on mangabey behavior and risk of extinction.

The Tana mangabey's behavioral and dietary flexibility enables it to buffer fluctuations in resource availability in a highly seasonal habitat and to adapt to large-scale habitat change. Mangabeys forage and eat more, and show extended infant dependency in response to changes in fruit distributions and lower fruit availability. A dietary shift between 1973-74 and 1988-89 from primarily ripe fruits to unripe seeds and invertebrates may constitute the best alternative strategy when ripe fruits are less available. Mangabey ranging patterns are influenced by a complex interaction of the spatial and temporal distribution of foods, forest patch size, group size, and intergroup interactions. Seasonal variation in food availability and distribution result in facultative defense of space by mangabeys.

The Tana mangabey's endangered status is primarily the result of the highly restricted distribution of Tana forest habitat and the rapid destruction of this habitat. Degradation of the remaining forests may result from non-sustainable human exploitation of forest species such as the palm, Phoenix reclinata. Results of demographic and genetic models suggest that the mangabey is at risk of losing genetic variation and has a high probability of extinction over the next 50-100 years given its present population status. A conservation strategy should incorporate measures for habitat preservation and enrichment. Because the

mangabey is a generalist species that easily exploits new habitat, it should respond well to habitat management.

CHAPTER ONE

INTRODUCTION

The Tana River crested mangabey, or Tana mangabey, (Cercocebus galeritus galeritus Peters 1879) is a rare and highly endangered cercopithecine monkey (IUCN 1976, Lee et al. 1988) found only in small forest patches of the Tana floodplain in north-eastern Kenya (Homewood 1976; Figure 1.1). Mittermeier (1981) ranked C. g. galeritus among the most endangered primates in the world, and the IUCN/SSC Primate Specialist Group listed it in the highest priority category for conservation (Oates 1985). These rankings were based on the small population size of C. g. galeritus, its highly restricted range, and the present threats to its habitat. C. g. galeritus experiences many of the classic factors contributing to endangerment: it has a small population size, is highly restricted in range, occupies a naturally patchy habitat that is becoming increasingly fragmented by human exploitation, and has experienced a population decline despite the creation of a reserve for its protection (Eisenberg 1980, Terborgh and Winter 1980).

The Tana mangabey, is thought to be a relict population of a once widely distributed species (Homewood 1975, 1976);

Figure 1.1. Adult male Tana River crested mangabey, Cercocebus galeritus galeritus, seated in a Hypheane compressa palm.

other subspecies, C. g. chrysogaster and C. g. agilis inhabit the Congolese forest block from Cameroon through Gabon, Congo (Brazzaville), and Zaire (Dandelot 1974, Lee et al. 1988). A fourth subspecies, C. g. sanjei, occurs in the Uzungwa Mountains of Tanzania (Homewood and Rodgers 1981, Lee et al. 1988). All subspecies of C. galeritus are semi-terrestrial and broadly similar in ecology and social behavior (Homewood 1975, Quris 1975) but vary in morphology. Dobroruka and Badalec (1966) and Groves (1978) have classified the Tana mangabey as a separate species based on differences in skull morphology. Irrespective of the taxonomy used, the important point is that the Tana mangabey is a geographically, and perhaps genetically, distinct population and should be considered separately from its conspecifics in the conservation arena.

The Tana mangabey occurs only within a 60 km stretch of the lower Tana River (Andrews et al. 1975, Homewood 1976) where ground-water seepage from the river is sufficient to support patches of riverine forest in a region of otherwise semi-arid bushland. Within the mangabeys' range there are an estimated 65 forest patches, averaging 35 ha in size (range <10-625 ha; Marsh 1978a, 1986), separated by stretches of deciduous woodland, bush, and grass. Forest patches, or fragments, result in part from changes in the river's course and patterns of flooding. Changes in the river's course during high floods leaves some forests far from the life-

supporting ground-water supply; others are cut and eroded by the scouring action of the river.

In recent years, natural forest fragmentation has been exacerbated by increasing human exploitation and land use (Homewood 1975, 1976; Hughes 1985, 1987, Kinnaird et al. 1990, Marsh 1986). An increasing local population (e.g., the number of families in one village, Nkano, increased from 1 to 7 between 1974 and 1986; personal observation T.T. Struhsaker), dependent on slash-and-burn agriculture, has resulted in increases in forest clearing and tree felling for houses and dugout canoes (Kinnaird et al. 1990). Medley (1990) showed a 56% reduction in forest area and fragmentation of 5 forest areas into 15 patches between 1960 and 1975. This loss was attributed, in part, to changes in the rivers course (Medley 1990), and to the destruction of forest for agriculture (Decker 1989).

Forests also have been cleared for large-scale irrigation schemes (Medley et al. 1989), and possibly have experienced a reduction in regeneration due to alterations in the rivers flow by upstream dams (Hughes 1985, 1990, Lee et al. 1988, Marsh 1986). Although changes in the flooding regime due to upstream dams have not been verified, Hughes (1985, 1990) has speculated that a reduction in peak floods due to damming will reduce the sediment/nutrient load and the frequency of meander formation and cut-off, thereby reducing the dynamic nature of the floodplain and the

occurrence of favorable conditions for seed germination and seedling establishment. Data from Medley (1990) indicate that upstream dams may be having an effect; the Tana River has shortened its course in recent years as a result of less meandering and sediments loads delivered during floods have declined. Agricultural practices also influence forest regeneration. Sites of active forest regeneration (i.e. point-bars) are selected for farming because much of the crop production by the local people is dependent on biannual flooding and the nutrient rich soils near the river.

The Tana River National Primate Reserve (TRNPR; Figure 1.2) was gazetted in 1976 by the government of Kenya to protect the best remaining stands of riverine forest and populations of the Tana River crested mangabey and red colobus monkey (Colobus badius rufomitratus). At the time of establishment, the reserve occupied approximately 171 km^2 of forest, dry woodland and savanna habitat on the east and west banks of the river (Marsh 1976). The forest habitat covered an estimated 17.5 km^2, broken into approximately 40 patches. In the 15 years since the establishment of the reserve, there has been a decline in forest area and increased fragmentation of the remaining forest stands (Kinnaird et al. 1990, Medley 1990). Primate populations also have declined by an estimated 83% for the red colobus (Marsh 1986, Decker 1989) and 25-45% for the mangabey (Chapter 6, Marsh 1986). The mangabey population

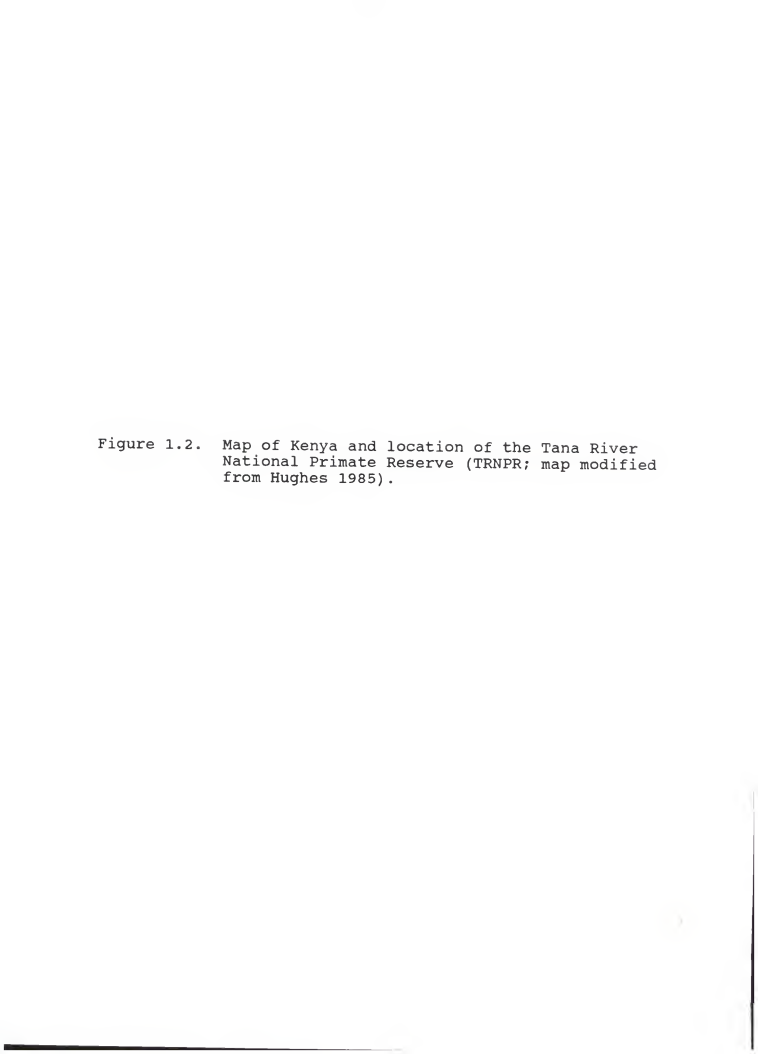
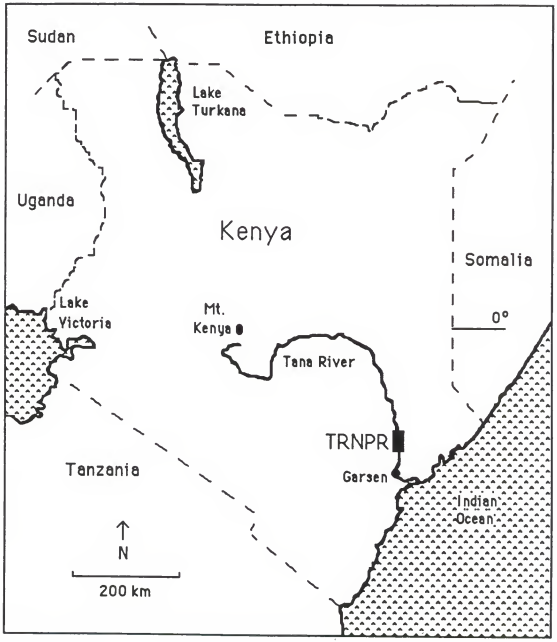


Figure 1.2. Map of Kenya and location of the Tana River National Primate Reserve (TRNPR; map modified from Hughes 1985).


Sudan
Ethiopia
Lake
Turkana
Uganda
Kenya
Somalia
Lake
Victoria
Mt.
Kenya
0°
Tana River
TRNPR
Tanzania
Garsen
Indian
Ocean
N
200 km

declined through a loss in the total number of groups, but the remaining groups showed no significant changes in size (Decker and Kinnaird 1990).

Kinnaird et al. (1990) speculated that the extensive loss of forest in the late 1960s led to a compression of the primate populations and unusually high population densities. In the subsequent 15-20 years these populations were believed to have declined and stabilized at levels in equilibrium with the new carrying capacity of the reduced forest area. Loss of forest area likely was exacerbated by reduction in habitat quality due to forest senescence (Hughes 1985, Marsh 1986) and possibly, by severe drought conditions in the early 1980s (Decker and Kinnaird 1990, Marsh 1986).

The present study examines the effects of habitat change on mangabey behavior and demography. The underlying theme of the dissertation is comparative, using baseline data on behavior and demography collected during a 1973-74 study by Homewood (1976), the only other study to date of the Tana mangabey. Comparison of my data with that of Homewood's (1976) allowed me to address questions concerning the loss of mangabey groups and effects of habitat change (e.g. loss of forest area and reductions in important mangabey diet species) on mangabey activity budgets, diet, ranging behavior, and risk of extinction. Detailed analysis of ecological and behavioral data collected during 1988-89 also

provided measures of variance in mangabey behaviors due to seasonal habitat change alone.

I begin in Chapter 2 by describing the abundance and distribution of important mangabey fruit resources and examining associations between the temporal availability of these resources and various environmental parameters. I also examine changes over the 15-year period in the temporal pattern of fruit availability. In Chapter 3, I investigate the effect of changes in forest structure and the food resource base on activity budgets. I also examine the temporal distribution (diurnal and seasonal) of activity patterns and the influence of diet on time budgets. In Chapter 4, I present an example of the impact of human exploitation of forest products on mangabeys. Specifically, I present data on competing uses of an important mangabey diet species, Phoenix reclinata, by mangabeys and humans. I quantify mangabey ranging patterns and defense of space in Chapter 5 and incorporate data from Chapters 2 and 3 to test the influence of seasonal changes in food availability and distribution on variation in defense of space by mangabeys. In Chapter 6, I present 2 approaches, demographic and genetic, for estimating population sizes necessary for the long-term persistence of the Tana mangabey. In this chapter, I evaluate the mangabey's risk of extinction by comparing derived population sizes with present population estimates. I summarize in Chapter 7 the major results of the body of

the dissertation and broadly discuss management recommendations.

CHAPTER TWO

ABUNDANCE AND DISTRIBUTION OF FRUIT RESOURCES IN THREE TANA RIVERINE FORESTS

Introduction

Temporal patterns of resource abundance and scarcity, coupled with the spatial distribution of fruit trees, are considered crucial to molding the ranging and foraging behaviors of frugivorous birds and primates (Chivers and Raemaekers 1980, Leighton and Leighton 1983, Terborgh 1983, Levey 1988). In most tropical trees, flowering and fruiting is episodic and seasonal peaks in fruit abundance have been recorded for many forests of the Neotropics (Foster 1974, Terborgh 1983, Levy 1988) and Old World tropics (Koelmeyer 1960, Medway 1972, Struhsaker 1975, Leighton and Leighton 1983, Gautier-Hion et al. 1985, van Schaik 1986). The timing of flowering and fruiting in tropical trees has been ascribed to climatic, edaphic and biotic factors (Rathche and Lacey 1985). In most tropical forests, variation in rainfall appears to be the most significant climatic factor influencing the phenologies of flowering and fruiting (Foster 1974, Hilty 1980, Borchert 1983), although the relationship between rainfall and plant reproduction is

variable in less seasonal forests (Hilty 1980, Heideman 1989). The phenological patterns of seasonal, ground-water dependent forests are not well documented and may be influenced more strongly by variation in river water level than other climatic factors.

The Tana River forests occur in a semi-arid environment with low annual rainfall (about 400 mm/year) and are dependent on ground-water from the river for their existence (Homewood 1976, Marsh 1976, Hughes, 1985). The occurrence of ground-water forest communities along the Tana appears to be related to the forest height above flood levels and duration of flooding, soil texture and therefore ability to hold water, soil chemistry, age of substrate and the history of human activities within the forest (Hughes 1985).

Little information exists on the influence of forest fragmentation, isolation or habitat change on tree phenologies. Increased leaf fall has been noted in Brazilian forests after fragmentation (Lovejoy et al. 1986) but even qualitative changes in plant reproduction have not been investigated. Varying degrees of habitat degradation, fragmentation and isolation within the Tana River forests over the last 15 years provide a basis for examining the effects of habitat change on plant reproduction.

In this chapter I describe the phenological and spatial patterns of fruit species eaten by Tana mangabeys in 3 forests. I derive 2 indices of monthly fruit production in

each forest and examine the associations between flowering and fruiting phenology, river flow, temperature and rainfall. I also make comparisons with similar data collected during 1973-74 (Homewood 1976) to determine if fruiting patterns differ between the 2 time periods.

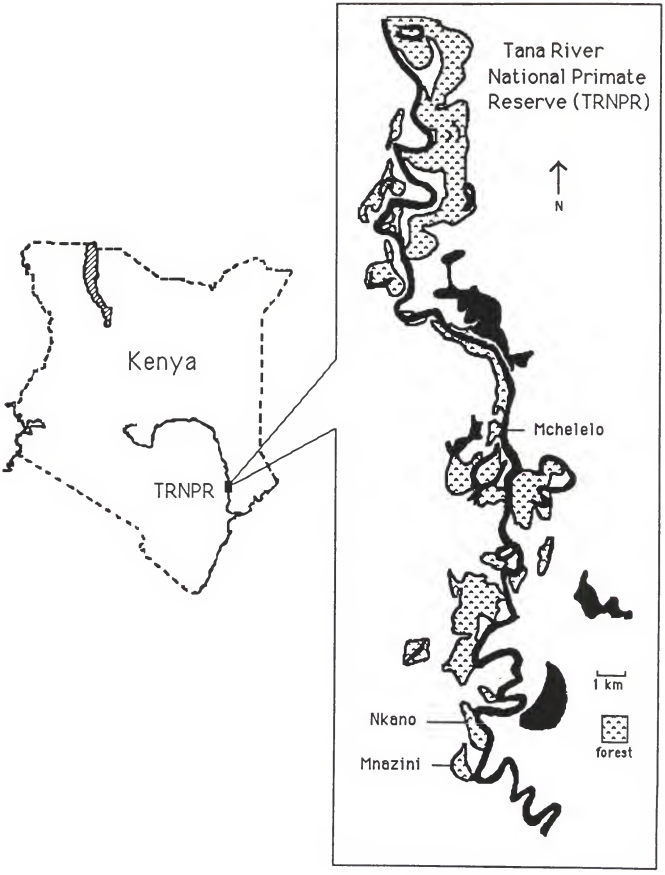
Methods

Study Sites

Three forests were chosen for intensive study: Mchelelo, Nkano and Mnazini (Figure 2.1). Baseline data were available for these forests from Homewood's (1976) 1973-74 study. The forests vary in size, vegetation, degree of flooding, human disturbance, and mangabey density. Mchelelo is a small forest (17 ha) with a diverse plant species composition. It is on a raised river levee and experiences minimal flooding. Mchelelo presently is occupied by 1-2 groups of mangabeys, depending on the season and is not disturbed by local people. Plant species composition has changed since the mid-1970s (Marsh 1986, Medley 1990) and several important mangabey food species have declined in abundance.

Nkano is a larger forest (38 ha) with a much less diverse plant species composition than Mchelelo (Homewood 1976, Medley 1990). Nkano presently is occupied by 2 mangabey groups and experiences a high degree of flooding and human exploitation. Although forest area in Nkano has decreased by an estimated 24% due to a fire in 1981 (Marsh

Figure 2.1. Map of the study area showing the Mchelelo, Mnazini, and Nkano forests within the Tana River National Primate Reserve.


Tana River
National Primate
Reserve (TRNPR)
N
Kenya
TRNPR
Mchelelo
1 km
Nkano
Mnazini
forest

1986, Decker 1989), plant species composition has not changed significantly since the mid-1970s (Medley 1990).

The 35 ha Mnazini forest is less than 0.5 km south of the Nkano forest, being separated from it by an old river course and an area of grassland. Mnazini is a low diversity forest (Homewood 1976, Medley 1990) that experiences high levels of flooding and human exploitation. The forest has decreased in size since the mid-1970s by approximately 50% due to floods and fires in 1982 and 1983, respectively. The number of mangabey groups in Mnazini has declined from 2 to 1 since the mid-1970s.

The climate is strongly seasonal. Rainfall averages 400 mm per year, most of which falls during the long rains (March-May) and the short rains (November-January), with intervening dry periods generally occurring during February (inter-rains) and June-October (dry season) (Hughes 1984). Floods are highly variable in intensity and timing but in general, water levels peak during the long and short rains (Hughes 1984).

Abundance and Distribution of Resources

Density. I enumerated selected tree species in 2 of the 3 study sites where mangabey groups were intensively studied (Mchelelo and Nkano) to calculate the abundance and describe the dispersion patterns of mangabey foods. Species were selected based on their importance in the diet during 1973-74 (Homewood 1976) or the present study. Only those trees of

reproductive size for each species were enumerated. Foot trails cut along compass bearings at 50m intervals were used to delineate quadrats of 0.25 ha. I enumerated 23 plant species within 65 quadrats (16.25 ha) for Mchelelo and 14 species within 54 quadrats (13.5 ha) for Nkano. Nine species present in Mchelelo were not found in Nkano. Average density was calculated by summing the number of individuals for a particular species in all quadrats and dividing by the total number of hectares sampled.

Spatial Distribution. I used Morisita's (1959) index of spatial pattern ($I_{\S}$) to measure the distribution of each species in the two forests. I chose Morisita's index over the more commonly used variance to mean ratio because many of the species I considered had calculated means less than 1.0 individual/ha. Greig-Smith (1983) has shown the variance to mean ratio to behave erratically when the mean is less than 1.0. Morisita's index provides a measure of the extent to which individuals of a particular species are nonrandomly distributed among identically-sized quadrats. The index is calculated as

$$I_{\S} = [\Sigma n_i(n_i - 1)/n(n-1)]\ N$$

where n_i is the number of individuals in the i^{th} quadrat, n is the total number of individuals in all quadrats, and N is the number of quadrats. Morisita's $I_{\S}$ ranges from 1/N to N; values approaching 1.0 indicate a random distribution and those less than or greater than 1.0 indicate regular and

patchy distributions, respectively. Deviation of the index from unity is tested with the F statistic.

Although Morisita's Index is relatively independent of quadrat size, Poole (1974) suggests that quadrats be large enough to contain at least one individual of one of the more common species. A quadrat size of 0.25 ha meets this requirement: the first and third most abundant species in Mchelelo forest, Phoenix reclinata and Hyphaene compressa, occur at least once in over 90% and 70% of the quadrats, respectively; at least one individual of one of the 3 most abundant species occurs in over 90% of the quadrats. The 3 most common species in Nkano forest, Alangium salviifolium, Phoenix reclinata and Pachystela msolo, all occur in over 90% of the quadrats and all quadrats contain at least 1 individual of 1 of these species.

Temporal Distribution. Temporal fluctuations in the availability of flowers and fruits were tabulated for 240 individuals in 16 species within the 3 forest areas: 126 individuals in 15 species for Mchelelo forest, 49 individuals in 9 species for Nkano forest, and 65 individuals in 8 species for Mnazini South forest (Table 2.1). I chose the species based on their presence in each study site and their importance as mangabey foods (Homewood 1976). The more common species were represented by at least 10 individuals; species with fewer than 10 individuals in the study areas were represented by the total number of

Table 2.1. Composition of mothly phenology sample by species for Mchelelo, Nkano and Mnazini forests.

Taxon	Number of Individuals		
	Mchelelo	Nkano	Mnazini
ALANGIACEAE			
Alangium salvifolium	10	5	-
ANACARDIACEAE			
Sorindeia madagascariensis	10	-	8
APOCYNACEAE			
Saba comorensis	7	3	8
EBENACEAE			
Diospyros mespiliformis	13	5	9
FLACOURTIACEAE			
Oncoba spinosa	10	-	
GUTTIFERAE			
Garcinia livingstonei	9	-	10
MIMOSACEAE			
Acacia robusta	10	-	10
Albizia gummifera	10	-	-
MORACEAE			
Ficus bubu	1	3	0
Ficus bussei	1	-	
Ficus natalensis	6	7	
Ficus sycomorus	10	8	7
PALMAE			
Hyphaene compressa	11	-	-
Phoenix reclinata	10	7	3
SAPOTACEAE			
Mimusops fruticosa	8	-	10
Pachystela msolo	-	-	10

individuals present. I chose only those individuals believed to be of a species' reproductive size and individuals whose canopies were relatively easy to view.

The phenological state of each individual was assessed monthly for Mchelelo (n=19 months), Nkano (n=17 months) and Mnazini (n=13 months) beginning October 1987. I used a 0-5 scale developed and used by Homewood (1976) in 1973-74 to visually assess the presence of flowers and ripe and unripe fruits on each individual. The scale is expressed as a proportion of the total canopy covered by flowers or fruits, where 0=no flowers or fruits, 1=1-20% coverage, 2=21-40% coverage, 3=41-60% coverage, 4=61-80% coverage and 5=81-100% coverage. Flowers and fruits were examined separately, each receiving a potential maximum score of 5.

Two indices of flower and fruit availability were calculated for each study forest using the 0-5 fruit scale. The first index is comparable to that used by Homewood (1976) and provides a relative measure of variation in flowering and fruiting. This index is calculated by pooling monthly flower or fruit scores for individuals of each species and averaging to give a mean species score for each month. An index of total monthly flowering or fruiting is calculated by summing monthly means for all species and dividing by the number of species in the sample.

The second index, used only for fruits, considers species differences in abundance and productivity and

provides an indication of monthly fruit biomass production. The index incorporates estimated numbers of fruits produced by a species during maximum fruit production, the estimated weight of fruits or fruit parts eaten by mangabeys, and the abundance of reproductive individuals. Fruit biomass indices were calculated for 4 categories of species, depending on how fruits were distributed throughout the canopy. Species bearing fruits primarily on the outer surface of the canopy (n=11) were categorized as surface fruiters. Species bearing fruits along their branches, either in clusters or evenly, were classified as ramiflorous fruiters (n=4). Palms (n=2) and lianas (n=1) each were classified separately because they do not have identifiable canopies.

I counted fruits only when individuals received the maximum phenological score of 5; this limited my sample size for some species because certain individuals were never scored as a 5. I estimated the number of fruits for all categories except the palms by counting the number of fruits visible within an approximately 1 m^3 field of vision of binoculars. One count in the top, middle and lower sections of the canopy or liana "tangle" was made for each individual and an average was taken. Fruits of the 2 palm species were counted directly for a minimum of 3 infructescenses. The numbers of fruits for the 3 infructescenses were averaged and multiplied by the total number of infrutescenses present. For Hyphaene compressa, a palm that branches and

has multiple crowns, the above value was multiplied by the number of crowns per individual.

Fruit counts for all species, excluding palms, were multiplied by an estimate of relative food-producing area to calculate the total number of fruits potentially produced by an average individual of a particular species. Fruit producing area was calculated using surface area and volume formulas for an open-bottomed cylinder, a shape that best approximates a variety of differing tree shapes (Appendix A). Surface areas were calculated for the category of species bearing their fruits primarily on the surface of the canopy and volumes were calculated for ramiflorous species. Branches of ramiflorous species were subjectively estimated to occupy little over 1/4 of the entire volume of the canopy; volume estimates, therefore, were divided by 4. The food-producing area of the liana species, which grows over the top of tree canopies, was calculated by estimating the amount of surface area of the tree canopy covered by the liana. I did not correct for canopy size in palms because a more direct count of fruit numbers was possible.

Samples of 10 or more fruits were collected and weighed from a maximum of 10 individuals per species. Only those fruit parts consumed by mangabeys were weighed and parts were weighed only during the stage of ripeness when mangabeys were feeding on them. Weights were averaged for individuals and individual averages were pooled to calculate

a species mean. The density of potentially reproductive individuals in each species for Mchelelo and Nkano study sites were taken from the species enumerations described above. Species densities for Mnazini were taken from Medley (1990).

A final monthly biomass (kg/ha) index of fruits of species sampled was calculated as:

$$FB = [\Sigma\{(X_{si}*D_{si}*SA_{si}*FP_{si})/I_{si}\}] + [\Sigma\{(X_{ri}*D_{ri}*V_{ri}*FP_{ri})/I_{ri}\}] + [\Sigma\{(X_{pi}*D_{pi}*FP_{p}i)/I_{pi}\}] + [\Sigma\{(X_{li}*D_{li}*SA_{li}*FP_{li})/I_{li}\}]$$ where

X = monthly fruit score for species i / 5 (to scale the scores to maximum production);

I = number of individuals scored for species i;

D = density of species i per hectare;

SA = surface area of species i;

V = branch volume of species i;

FP = total fruit production measured as mean fruit count * mean fruit weight of species i;

and subscripts s, r, p and l denote surface, ramiflorous, palm and liana categories, respectively.

Environmental Correlates with Flowering and Fruiting

I examined associations between 3 environmental parameters and the temporal patterns of flowering and fruiting in the 3 study sites. A Spearman's rank correlation analysis (Siegel 1956) was conducted to examine possible

associations between rainfall, riverflow and temperature, and flower and fruit scores for trees and lianas for each forest and all forests combined. I conducted separate analyses for flowers and fruits for all species combined. For fruits, I examined seasonal and continuous fruiting species separately, and ripe versus. unripe fruits. Because flowering occurred as much as 3 months prior to fruiting, monthly flowering, rainfall and river flow data were lagged up to 3 months in each analysis. Associations between flowering and fruiting and environmental conditions during the months after flowering or fruiting were examined by advancing rain and river data by one month. I also conducted a multiple regression analysis to test whether the environmental parameters chosen explain a significant amount of variability in fruiting. A square root transformation was performed on monthly scores because they were discrete data (Sokal and Rohlf 1981). Monthly rainfall levels were recorded for Mchelelo and Nkano/Mnazini areas, and Tana River discharge levels for the Hola Station were obtained from the Kenya Water Department, Hydrology Section.

Comparisons with 1973-74

I compared monthly fruit scores for 9 species examined during this study and by Homewood in 1973-74 to determine if fruiting patterns varied between the 2 study periods. Seven species from Mnazini and 6 species from Mchelelo forest were compared. I subsampled from my 1987-89 data to correspond

with Homewood's 12 month data from Mnazini forest and 7 month data from Mchelelo forest. Kolmogrov-Smirnov two-sample tests (Hollander and Wolfe 1973) were performed by species to test for differences in the distributions of fruiting between the 2 study periods. Wilcoxon signed-ranks tests also were performed by species to test whether fruit scores were consistently higher during 1 study period than the other.

Results

Abundance and Spatial Distribution of Resources

Density values ranged widely for enumerated species both within and between forests (Table 2.2). Over 50% of the species enumerated in Mchelelo (n=13 of 25) and Nkano (n=8 of 15) were rare, occurring at densities of less than 1 individual per ha. The palm, Phoenix reclinata, was one of the most common species, occurring at the highest and second highest densities (193.6 and 101.6 individuals/ha) of all species in Mchelelo and Nkano, respectively. Alangium salviifolium, an understory species, also occurred at very high densities (33.6-112.3 individuals/ha) in both forests. Five species present in both forests (Pachystela msolo, Ficus sycomorus, Alangium salviifolium, Aporrhiza paniculata and Saba comorensis) occurred at much higher densities in Nkano than Mchelelo; 4 additional species (Sorindeia

Table 2.2. Density of reproductive trees and lianas enumerated in 16.32 ha of Mchelelo forest and 13.45 ha in Nkano forest, and the degree of clumping of each species using Morisita's index (I_δ). If I_δ is significantly greater or less than unity using the F-test, the species is considered clumped or evenly distributed in space, respectively. If I_δ is not significantly different from unity than the species is considered randomly distributed.

		Mchelelo			Nkano		
Taxon	Code	Density	I_δ	F-test (p)	Density	I_δ	F-Test (p)
ALANGIACEAE							
Alangium salvifolium	AS	33.56	2.71	<0.001	112.26	1.27	<0.001
ANACARDIACEAE							
Lannea stuhlmannii	LS	0.55	1.81	ns	0.30	27.00	<0.001
Sorindeia madagascariensis	SO	6.74	2.16	<0.001	0.15	54.00	<0.001
APOCYNACEAE							
Rauvolfia mombasiana	RM	52.01	3.68	<0.001	-	-	-
Saba comorensis	SF	0.86	3.57	<0.005	6.77	1.31	<0.005
BORAGINACEAE							
Cordia goetzei	CG	4.59	1.52	<0.001	0.00	-	-
CAESALPINACEAE							
Cynometra webberi	CW	0.43	9.29	<0.001	0.00	-	-
Tamarindus indica	TI	0.49	4.64	<0.001	0.00	-	-
EBENACEAE							
Diospyros mespiliformis	DM	7.72	1.51	<0.001	1.19	1.35	ns
FLACOURTIACEAE							
Oncoba spinosa	OS	6.49	2.67	<0.001	0.45	14.40	<0.001
GUTTIFERAE							
Garcinia livingstonei	GL	1.72	8.60	<0.001	0.37	5.40	ns
MIMOSACEAE							
Acacia robusta	AR	0.67	3.55	<0.001	0.00	-	-
Albizia gummifera	AG	1.65	2.78	<0.001	0.00	-	-
Albizia glaberrima	AL	0.55	3.61	ns	0.00	-	-
MORACEAE							
Ficus bubu	FU	0.06	-	-	0.89	2.45	ns
Ficus bussei	FB	0.06	-	-	0.00	-	-
Ficus natalensis	FN	0.55	0.00	ns	0.45	0.00	ns
Ficus sycomorus	FS	1.16	1.14	ns	4.68	3.98	<0.001
PALMAE							
Hyphaene compressa	HC	17.45	2.48	<0.001	0.00	-	-
Phoenix reclinata	PR	193.57	1.39	<0.001	101.64	1.90	<0.001
SAPINDACEAE							
Aporrhiza paniculata	AP	1.64	4.94	<0.001	8.70	1.90	<0.001
Blighia unijugata	BU	0.86	17.86	<0.001	0.15	0.00	ns
SAPOTACEAE							
Mimusops fruticosa	MF	0.86	1.43	ns	0.00	-	-
Pachystela msolo	PB	0.31	0.00	ns	35.99	1.35	<0.001
STERCULIACEAE							
Sterculia appendiculata	SA	0.89	5.91	<0.001	0.07	-	-

madagascariensis, Diospyros mespiliformis, Oncoba spinosa and Garcinia livingstonei) occurred at much higher densities in Mchelelo than Nkano (Table 2.2).

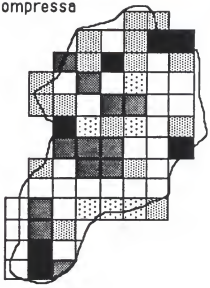
The majority of species in both forests were patchily or randomly distributed in space and no species showed a uniform spatial pattern (Table 2.1, Figures 2.2-2.4). The tendency towards patchy distributions of species was consistent on a larger spatial scale: quadrats with high numbers of individuals of a species tended to be clumped throughout the forests (Figures 2.2 and 2.3). Five species showed different patterns of spatial distribution between the 2 forests. Diospyros mespiliformis, Garcinia livingstonei, and Blighia unijugata occurred in clumps in Mchelelo but were randomly distributed in Nkano. Pachystela msolo and Ficus sycomorus, on the other hand, occurred in clumps in Nkano but were randomly distributed in Mchelelo. These apparently random distributions, however, may be an artifact of small sample size.

Temporal Distribution of Resources

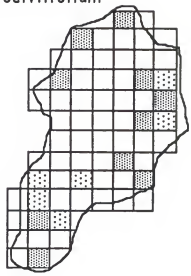
Patterns of flowering and fruiting. Flower and fruit scores averaged over all species by month suggest seasonality of flowering and fruiting in the 3 forests (Figures 2.5 and 2.6). Increased flowering occurred from August to December with minor increases in February and March. Fruiting was high from January to May of 1988, and November to March of 1988-89; low levels of fruiting

Figure 2.2. Number of individuals/0.25 ha quadrat of 4 common species within Mchelelo forest showing clumped spatial distributions.
a) Hyphaene compressa; b) Alangium salviifolium; c) Phoenix reclinata; d) Oncoba spinosa.

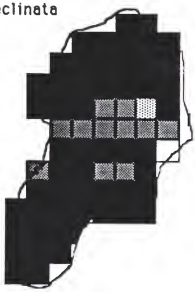
Hyphaene compressa



Alangium salviifolium



Phoenix reclinata



Oncoba spinosa

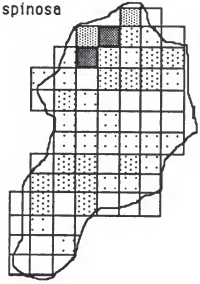
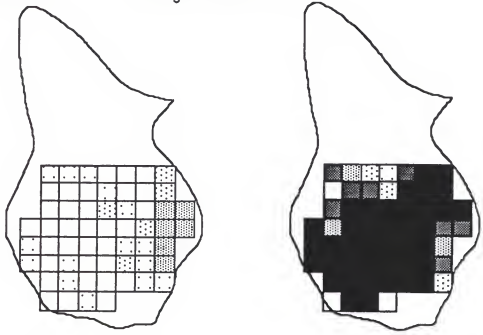


Figure 2.3. Number of individuals/0.25 ha quadrat of 4 common species within Nkano forest showing clumped spatial distributions.
a) Ficus sycomorus; b) Alangium salviifolium; c) Phoenix reclinata; d) Pachystela msolo.

Ficus sycomorus

Alangium salviifolium



Phoenix reclinata

Pachystela msolo

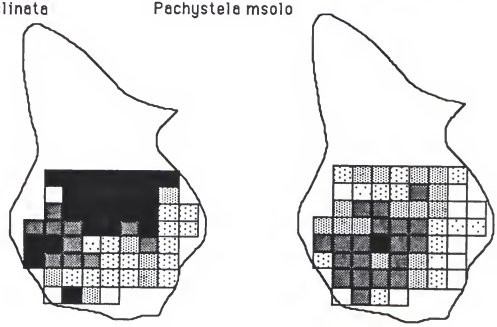
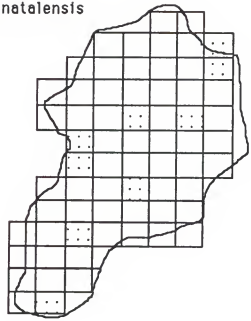
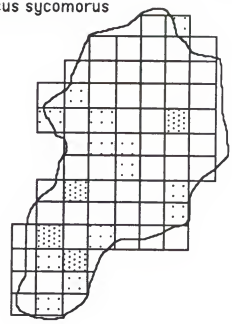


Figure 2.4. Examples of randomly distributed Ficus spp. a) Ficus natalensis in Mchelelo forest; b) Ficus sycomorus in Mchelelo forest; c) Ficus natalensis in Nkano forest.

Ficus natalensis



Ficus sycomorus



Ficus natalensis

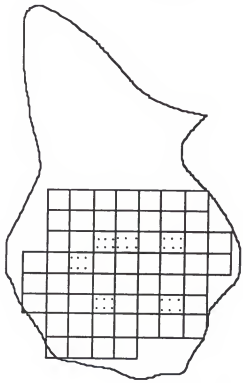


Figure 2.5. Mean flower scores averaged over all species by month.
a) Mchelelo forest; b) Nkano forest; c) Mnazini forest.

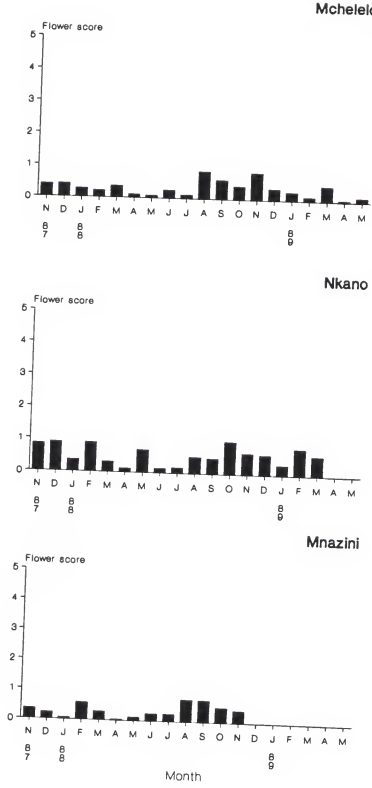
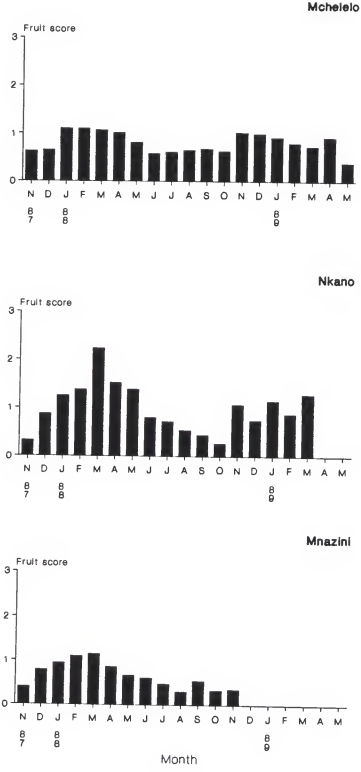

Mchelelo
Flower score
5
4
3
2
1
0
N D J F M A M J J A S O N D J F M A M
87
88
89
Nkano
Flower score
5
4
3
2
1
0
N D J F M A M J J A S O N D J F M A M
87
88
89
Mnazini
Flower score
5
4
3
2
1
0
N D J F M A M J J A S O N D J F M A M
87
88
89
Month

Figure 2.6. Mean fruiting scores averaged over all species by month.
a) Mchelelo forest; b) Nkano forest; c) Mnazini forest.


Mchelelo
Fruit score
3
2
1
0
N D J F M A M J J A S O N D J F M A M
87
88
89
Nkano
Fruit score
3
2
1
0
N D J F M A M J J A S O N D J F M A M
87
88
89
Mnazini
Fruit score
3
2
1
0
N D J F M A M J J A S O N D J F M A M
87
88
89
Month

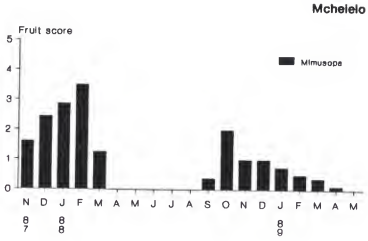
occurred from June to October in Mchelelo and Nkano and from July through November in Mnazini.

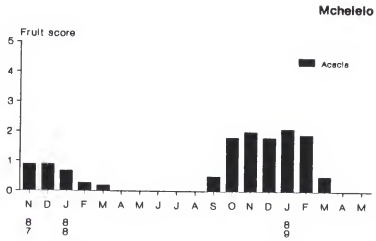
Several species showed seasonal patterns of fruiting (Figures 2.7-2.10). The majority of seasonal fruiters bore fruits only once in a year; however, individuals of 2 species (Sorindeia madagascariensis and Garcinia livingstonei) produced fruits twice within a year (Figure 2.8). Of the seasonal fruiters, only Phoenix reclinata and Diospyros mespiliformes produced fruit during the cool, dry months between June and September (Figures 2.9 and 2.10). Three species appeared to fruit continuously (Figures 2.11 and 2.12) due to 1) continuous production of fruit by all individuals (Oncoba spinosa and Ficus sycomorus); 2) retention of fruits over long periods of time (Hyphaene compressa); and 3) unsynchronized bouts of fruiting (Ficus natalensis).

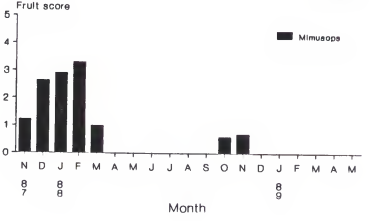
Species sampled in more than 1 of the forests tended to show similar patterns of fruiting among forests. One exception was the liana, Saba comorensis. Saba comorensis exhibited highly seasonal fruiting in Mnazini, seasonal but extended fruiting in Nkano, and continuous fruiting in Mchelelo (Figure 2.13).

Estimates of fruit biomass. Estimated maximum fruit numbers, fruit weight and canopy size varied widely between species and shape categories (Table 2.3), and strongly influenced monthly biomass indices of fruit (Figure 2.14).

Figure 2.7. Mean monthly fruit scores from Mchelelo and Mnazini forests for Mimusops fruticosa and Acacia robusta, seasonally fruiting species with 1 peak in fruiting per year.
a) Mimusops fruiticosa in Mchelelo forest; b) Acacia robusta in Mchelelo forest; c) Mimusops fruticosa in Mnazini forest; d) Acacia robusta in Mnazini forest.


Mchelelo
Frult score
Mimusops
N D J F M A M J J A S O N D J F M A M
87 88 89


Mchelelo
Frult score
Acacia
N D J F M A M J J A S O N D J F M A M
87 88 89


Mnazini
Frult score
Mimusops
N D J F M A M J J A S O N D J F M A M
87 88 89
Month

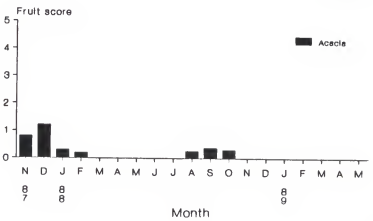
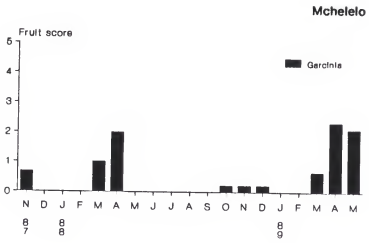
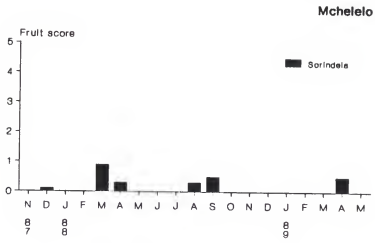
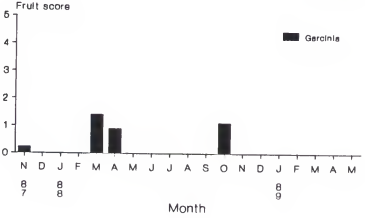

Mnazini
Frult score
Acacia
N D J F M A M J J A S O N D J F M A M
87 88 89
Month

Figure 2.8. Mean monthly fruit scores from Mchelelo and Mnazini forests for Garcinia livingstonei and Sorindeia madagascariensis, seasonally fruiting species with 2 fruiting peaks per year.
a) Garcinia livingstonei in Mchelelo forest; b) Sorindeia madagascariensis in Mchelelo forest; c) Garcinia livingstonei in Mnazini forest; d) Sorindeia madagascariensis in Mnazini forest.


Mchelelo
Fruit score
Garcinia
N D J F M A M J J A S O N D J F M A M
87 88 89


Mchelelo
Fruit score
Sorindeia
N D J F M A M J J A S O N D J F M A M
87 88 89


Mnazini
Fruit score
Garcinia
N D J F M A M J J A S O N D J F M A M
87 88 89
Month

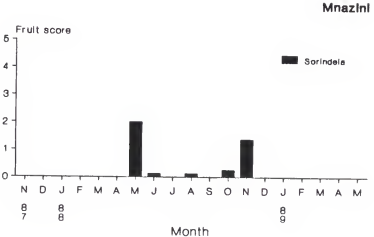

Mnazini
Fruit score
Sorindeia
N D J F M A M J J A S O N D J F M A M
87 88 89
Month

Figure 2.9. Mean monthly fruit scores for Phoenix reclinata.
a) Mchelelo forest; b) Nkano forest; c) Mnazini forest.

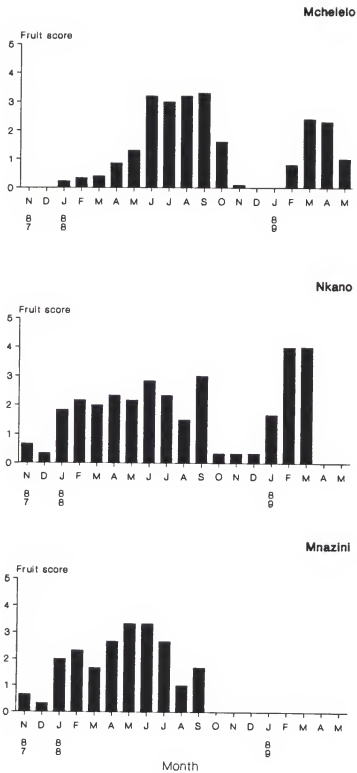

Mchelelo
Fruit score
5
4
3
2
1
0
N D J F M A M J J A S O N D J F M A M
87
88
89
Nkano
Fruit score
5
4
3
2
1
0
N D J F M A M J J A S O N D J F M A M
87
88
89
Mnazini
Fruit score
5
4
3
2
1
0
N D J F M A M J J A S O N D J F M A M
87
88
89
Month

Figure 2.10. Mean monthly fruit scores for Diospyros mespiliformes.
a) Mchelelo forest; b) Nkano forest; c) Mnazini forest.

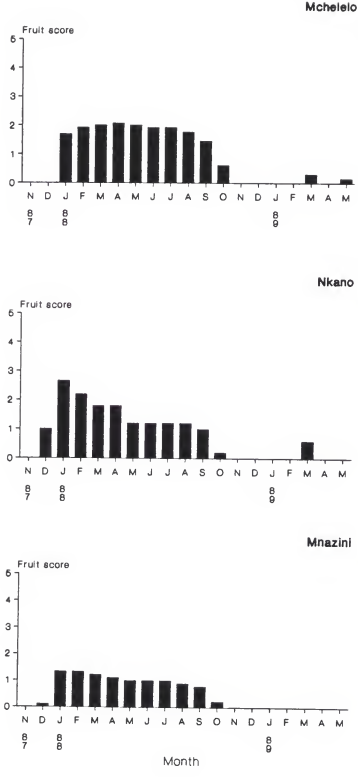
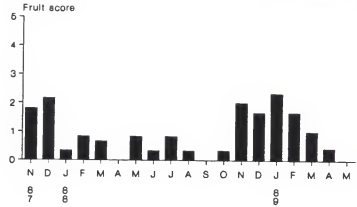
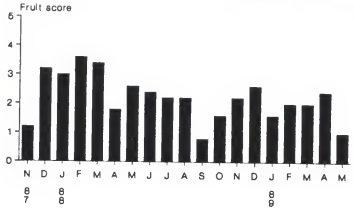

Mchelelo
Fruit score
0
1
2
3
4
5
N D J F M A M J J A S O N D J F M A M
87
88
89
Nkano
Fruit score
0
1
2
3
4
5
N D J F M A M J J A S O N D J F M A M
87
88
89
Mnazini
Fruit score
0
1
2
3
4
5
N D J F M A M J J A S O N D J F M A M
87
88
89
Month

Figure 2.11. Mean monthly fruit scores for 3 species showing patterns of continuous fruit production.
a) continuous fruiting due to asynchrony among individuals of the species (Ficus natalensis); b) continuous fruiting due to retention of fruits over time (Hyphaene compressa); c) continuous fruiting due to rapid turnover of fruits (Oncoba spinosa).

Ficus natalensis



Hyphaene compressa



Oncoba spinosa

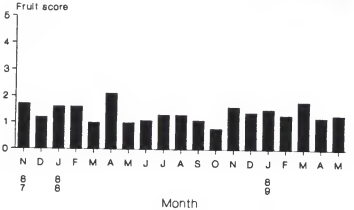


Figure 2.12. Mean monthly fruit scores for Ficus sycomorus. a) Mchelelo forest; b) Nkano forest; c) Mnazini forest.

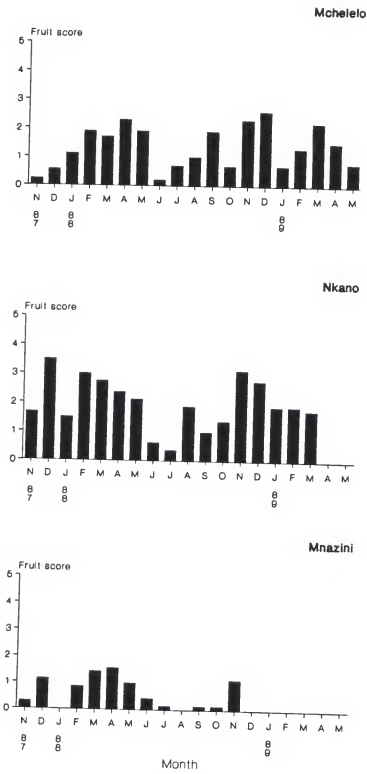

Mchelelo
Fruit score
0
1
2
3
4
5
N D J F M A M J J A S O N D J F M A M
87 88 89
Nkano
Fruit score
0
1
2
3
4
5
N D J F M A M J J A S O N D J F M A M
87 88 89
Mnazini
Fruit score
0
1
2
3
4
5
N D J F M A M J J A S O N D J F M A M
87 88 89
Month

Figure 2.13. Seasonality of mean monthly fruit scores for Saba comorensis in the 3 study forests. a) seasonal fruiting in Mnazini forest; b) seasonal but extended fruiting in Nkano forest c) continuous fruiting in Mchelelo forest.

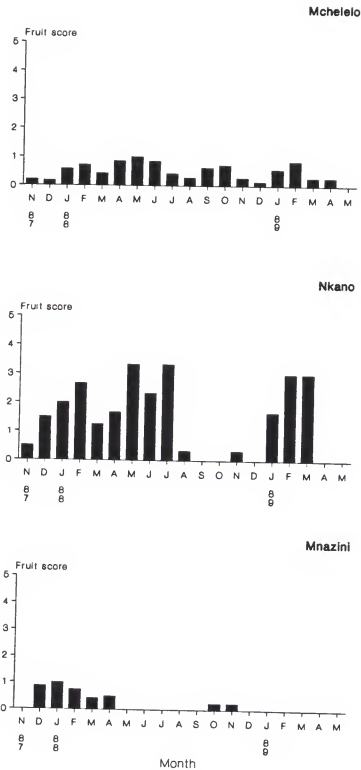
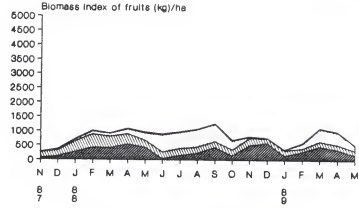

Mchelelo
Fruit score
5
4
3
2
1
0
N D J F M A M J J A S O N D J F M A M
87 88 89
Nkano
Fruit score
5
4
3
2
1
0
N D J F M A M J J A S O N D J F M A M
87 88 89
Mnazini
Fruit score
5
4
3
2
1
0
N D J F M A M J J A S O N D J F M A M
87 88 89
Month

Table 2.3. Estimated canopy surface area (S), canopy volume (V), mean fruit production (FN) and mean fruit weight (FW) for 16 species. Species are categorized into 4 groups: those that bear their fruits on the canopy surface (C) or along the branches of the tree (R), lianas (L) and palms (P).

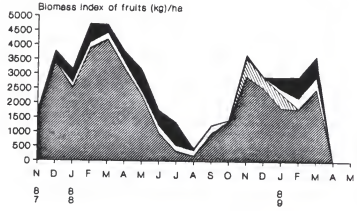
Taxon	Group	S(m^3)	V(m^3)	FN(m^3)	FW(gr)
Alangium salvifolium	C	125.9	-	48	0.86
Sorindeia madagascariensis	R	-	313.0	142	0.65
Saba comorensis	L	232.0	-	6	119.15
Diospyros mespiliformis	C	1016.3	-	47	1.27
Oncoba spinosa	C	74.3	-	12	29.07
Garcinia livingstonei	C	567.0	-	47	4.87
Acacia robusta	C	931.2	-	48	0.96
Albizia gummifera	C	731.6	-	26	0.70
Ficus bubu	R	-	412.0	122	7.75
Ficus bussei	C	1965.0	-	55	7.80
Ficus natalensis	C	1004.8	-	176	0.80
Ficus sycomorus	R		1345.0	90	7.86
Hyphaene compressa	P	-	-	980	6.88
Phoenix reclinata	P	-	-	11502	0.81
Mimusops fruticosa	C	695.8	-	67	6.18
Pachystela msolo	R		627.3	121	0.94

Figure 2.14. Contribution to monthly fruit biomass indices by different species categories. a) Mchelelo forest; b) Nkano forest; c) Mnazini forest.

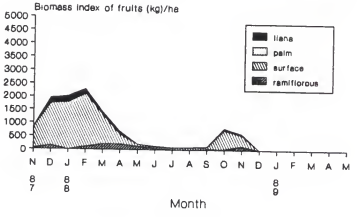
Mchelelo



Nkano



Mnazini

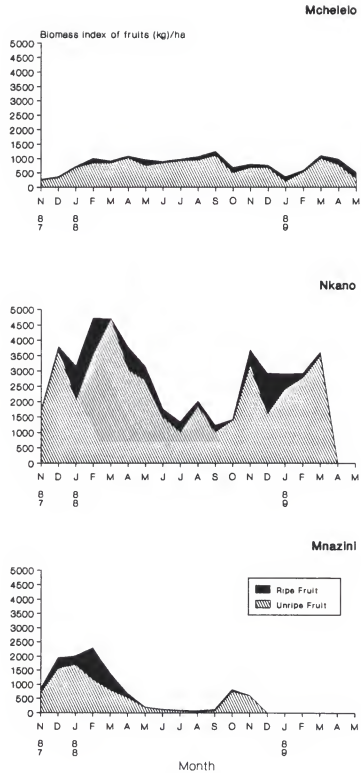


Palms, particularly Phoenix reclinata, often accounted for a large proportion of the monthly biomass indices in Mchelelo because of their potential for large fruit crops and their high density in the forest. Although ramiflorous species were not abundant in Mchelelo, their capacity for large fruit crops results in a relatively large contribution to the monthly biomass indices. In Nkano, ramiflorous species such as Pachystela msolo and Ficus sycomorus were abundant and they dominated the monthly biomass index.

Although fewer species were sampled in Nkano, the forest produced a much greater biomass of fruits than either Mchelelo or Mnazini for all months of the year with the exception of August. The high fruit biomass production by Nkano was primarily the result of high densities of Ficus sycomorus, a species that produces large fruit crops throughout the year, with a decline in production during June and July (Figure 2.12). Mchelelo had a more consistent production of fruits across the months due to the availability of palm fruits between May and October, a period of relative scarcity in the other 2 forests. Mnazini, with a low abundance of figs and palms, was more seasonal in fruit production than Mchelelo or Nkano and experienced a 4 month period (May-Aug) of fruit scarcity.

Unripe fruits contributed the most to the biomass index over all months in all study forests; ripe fruits were entirely unavailable during several months (Figure 2.15).

Figure 2.15. Contribution of ripe and unripe fruits to monthly fruit biomass index.
a) Mchelelo forest; b) Nkano forest; c) Mnazini forest.


Mchelelo
Biomass index of fruits (kg)/ha
5000
4500
4000
3500
3000
2500
2000
1500
1000
500
0
N D J F M A M J J A S O N D J F M A M
87 88 89
Nkano
5000
4500
4000
3500
3000
2500
2000
1500
1000
500
0
N D J F M A M J J A S O N D J F M A M
87 88 89
Mnazini
Ripe Fruit
Unripe Fruit
5000
4500
4000
3500
3000
2500
2000
1500
1000
500
0
N D J F M A M J J A S O N D J F M A M
87 88 89
Month

The predominance of unripe fruits may be the result of the time necessary to ripen a fruit crop and/or asynchronous ripening within individuals, and fruits being selectively chosen by animals as soon as they ripen. Nkano and Mnazini generally had larger biomasses of ripe fruits relative to Mchelelo, possibly due to the higher density of figs in Nkano and species such as Mimusops fruticosa and Garcinia livingstonei in Mnazini, that tend to ripen more synchronously.

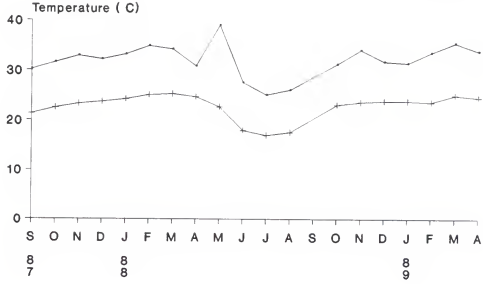
Environmental Correlates with Flowering and Fruiting

Temperature, rainfall and river flow showed strong seasonality. The hottest months occurred between November and April and the coolest months occurred between June and October (Figure 2.16). Rainfall was high during November and December and again from March-June (Figure 2.17). Rainfall in Nkano generally was higher than Mchelelo although there was a strong correlation between monthly totals for the 2 areas ($r=0.85$, $n=11$, $p<0.05$). River flow was highest April-June, 1988 and January-April, 1989 (Figure 2.18), and was correlated with the previous months rainfall in both areas ($r=0.72$ and 0.76 for Nkano and Mchelelo, respectively, $n=11$, $p<0.05$).

Flowering was negatively correlated with rainfall in Nkano ($r=-0.57$, $n=14$, $p<0.05$) and with river flow in Mchelelo ($r=-0.51$, $n=16$, $p<0.05$) and Mnazini ($r=-0.77$, $n=10$, $p<0.05$). When all 3 forests are combined, there were

Figure 2.16. Monthly mean minimum and mean maximum air temperature in degrees centigrade. a) Mchelelo forest; b) Nkano/Mnazini forest areas.

Mchelelo



Nkano

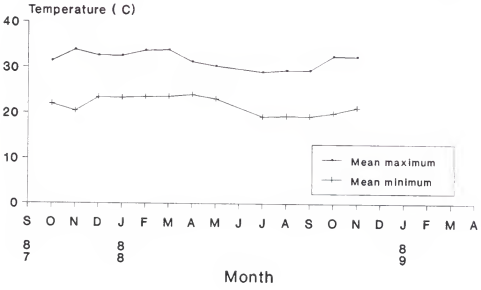
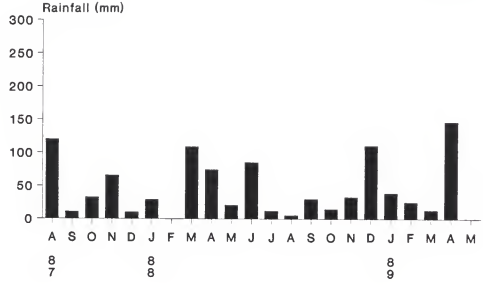


Figure 2.17. Total monthly rainfall in millimeters. a) Mchelelo forest; b) Nkano/Mnazini forest area.

Mchelelo



Nkano

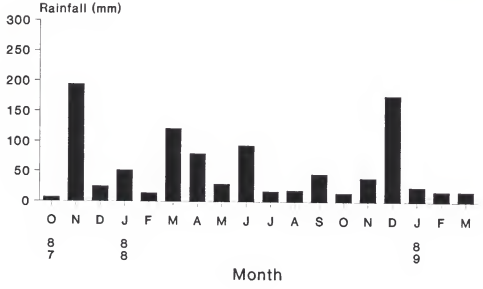
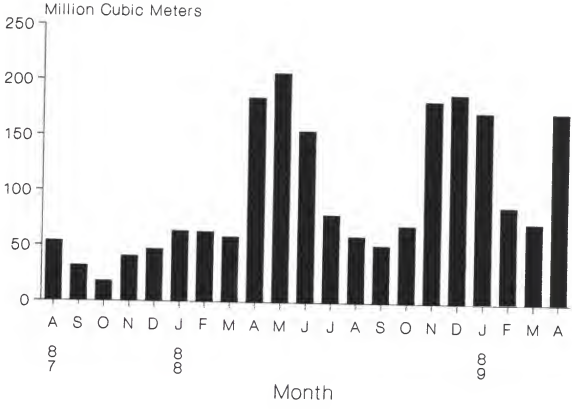


Figure 2.18. Mean monthly river flow for the Tana River Hola Station.


Million Cubic Meters
250
200
150
100
50
0
A S O N D J F M A M J J A S O N D J F M A
87
88
89
Month

significant negative correlations between flowering and both rainfall and river flow ($r=0.-41$ and -0.35 for rainfall and river flow, respectively, $n=41$, $p<0.05$). Correlations between flowering and fruiting were significant when flower scores were lagged by 3 months in Mchelelo, Nkano and for all 3 forests combined ($r=0.76$, $p<0.05$ for Mchelelo, $r=0.55$, $p<0.05$ for Nkano and $r=.45$, $n=41$, $p<0.05$ for all forests combined).

There were no consistent associations between monthly fruit scores and either rainfall or river flow for the 3 forests (Tables 2.4, 2.5 and 2.6). Minimum monthly temperature was positively correlated with monthly fruit scores for all species combined in the 3 separate forests. There were also positive correlations between minimum monthly temperature and scores from seasonal fruiting species in Nkano and Mnazini. When the palm, P. reclinata, was removed from the analysis, there were significant negative correlations between fruiting of seasonal species and river flow lagged by 3 months. Phoenix reclinata showed significant positive correlations with river flow lagged only by 1 or 2 months.

When data for all forests were combined, many of the results were consistent with the analysis performed on the forests separately (Table 2.7). There were significant positive correlations between fruit scores for continuous species and rainfall. Minimum monthly temperature showed

Table 2.4. Spearman's rank correlation coefficients for mean monthly environmental variables and mean monthly fruiting scores for Mchelelo forest. MINTEMP=minimum monthly temperature; RAIN=total monthly rainfall (mm); RAINLAG1, RAINLAG2 AND RAINLAG3=monthly rainfall lagged by 1,2, and 3 months, respectively; RAINADV=previous months' rainfall; FLOW=mean monthly river flow (mcm); FLOWLAG1, FLOWLAG2, FLOWLAG3=mean monthly river flow lagged by 1,2 and 3 months, respectively; FLOWADV=previous months' mean river flow.

	RIPE AND UNRIPE			RIPE ONLY			RIPE AND UNRIPE	RIPE AND UNRIPE
	Total	Continuous	Seasonal	Total	Continuous	Seasonal	Seasonal (w/o *P. reclinata*)	*P. reclinata*
MINTEMP	0.54*	ns	ns	ns	ns	ns	ns	ns
RAIN	ns	ns	ns	ns	ns	ns	ns	ns
RAINLAG1	ns	ns	ns	ns	ns	ns	ns	ns
RAINLAG2	ns	ns	ns	ns	ns	ns	ns	ns
RAINLAG3	ns	ns	ns	ns	ns	ns	ns	ns
RAINADV	ns	.74*	ns	ns	ns	ns	ns	ns
FLOW	ns	ns	ns	ns	ns*	ns	ns	ns**
FLOWLAG1	ns	ns	ns	ns	0.64*	ns	ns	0.78**
FLOWLAG2	ns	ns	ns	ns*	ns	ns	ns*	0.83**
FLOWLAG3	ns	ns	ns	0.48*	ns	ns	-0.59*	0.79**
FLOWADV	ns	ns	ns	ns	ns	ns	ns	ns

* p<0.05
** p<0.001

Table 2.5. Spearman's rank correlation coefficients for mean monthly environmental variables and mean monthly fruiting scores for Nkano forest. Variables defined in Table 2.4.

	RIPE AND UNRIPE			RIPE ONLY			RIPE AND UNRIPE	RIPE AND UNRIPE
	Total	Continuous	Seasonal	Total	Continuous	Seasonal	Seasonal (w/o *P. reclinata*)	*P. reclinata*
MINTEMP	0.72*	0.63*	0.61*	ns	ns	ns	0.74	0.75**
RAIN	ns	ns	ns	ns	ns	ns	ns	ns
RAINLAG1	ns	ns	ns	ns	0.60*	ns	ns	ns
RAINLAG2	ns	ns	ns	ns	ns	ns	ns	ns
RAINLAG3	ns	ns	ns	ns	ns	ns	ns	ns
RAINADV	ns	ns	ns	ns	ns	ns	ns	ns
FLOW	ns	ns	ns	ns	ns	ns	ns	ns
FLOWLAG1	ns	ns	ns	ns	ns	ns	ns	0.78**
FLOWLAG2	ns	ns	ns	ns	ns	ns	ns	0.83**
FLOWLAG3	ns	ns	ns	ns	ns	ns	-0.59*	0.79**
FLOWADV	ns	ns	ns	ns	ns	ns	ns	ns

* $p<0.05$
** $p<0.001$

Table 2.6. Spearman's rank correlation coefficients for mean monthly environmental variables and mean monthly fruiting scores for Mnazini forest. Variables defined in Table 2.4.

	RIPE AND UNRIPE			RIPE ONLY			RIPE AND UNRIPE	RIPE AND UNRIPE
	Total	Continuous	Seasonal	Total	Continuous	Seasonal	Seasonal (w/o *P. reclinata*)	*P. reclinata*
MINTEMP	0.58*	ns	0.58*	0.72**	0.60*	0.68*	0.58*	0.75**
RAIN	ns	ns	ns	ns	ns*	ns	ns	ns
RAINLAG1	ns	ns	ns	ns	0.60*	ns	ns	ns
RAINLAG2	ns	ns	ns	ns	ns	ns	ns	ns
RAINLAG3	ns	ns	ns	ns	ns	ns	ns	ns
RAINADV	ns	ns	ns	ns	ns	ns	ns	ns
FLOW	ns	0.78**	ns	ns*	0.57*	ns	ns	ns**
FLOWLAG1	ns	ns	ns	0.59*	ns	ns	ns	0.78**
FLOWLAG2	ns	ns	ns*	ns	ns	ns	ns**	0.83**
FLOWLAG3	ns	ns	-0.59*	-0.63*	ns	ns	-0.71**	0.79**
FLOWADV	ns	ns	ns	ns	ns	ns	ns	ns

* p<0.05
** p<0.001

Table 2.7. Spearman's rank correlation coefficients for mean monthly environmental variables and mean monthly fruiting scores for all forests combined. Variables defined in Table 2.4.

	RIPE AND UNRIPE			RIPE ONLY			RIPE AND UNRIPE	RIPE AND UNRIPE
	Total	Continuous	Seasonal	Total	Continuous	Seasonal	Seasonal (w/o *P. reclinata*)	*P. reclinata*
MINTEMP	ns	ns	ns	ns	ns	0.39*	0.53*	ns
RAIN	ns	ns	ns	ns	ns	ns	ns	ns
RAINLAG1	ns	ns	ns	ns	0.37*	ns	ns	ns
RAINLAG2	ns	ns	ns	ns	ns	ns	ns	ns
RAINLAG3	ns	ns	ns	ns	ns	ns	ns	0.46*
RAINADV	ns	ns	ns	ns	ns	ns	ns	ns
FLOW	ns	ns	ns	ns	ns	ns	ns	ns
FLOWLAG1	ns	ns	ns	ns	ns	ns	ns	0.39*
FLOWLAG2	ns	ns	ns	ns	ns	ns	-0.41*	0.51**
FLOWLAG3	ns	ns	-0.58	ns	ns	ns	-0.59*	0.34*
FLOWADV	ns	ns	ns	ns	ns	ns	ns	ns

* $p<0.05$
** $p<0.001$

significant positive correlations, and river flow lagged by 2 and 3 months showed significant negative correlations with seasonal fruiting species excluding P. reclinata. Combined P. reclinata scores for the 3 sites were significantly correlated with rainfall lagged by 2 months and river flow lagged by at least 1 month.

A multiple regression model incorporating minimum temperatures and river flow lagged by 3 months, the 2 variables most highly correlated with fruit scores, explained 25.7% of the variance in monthly fruit scores for seasonal species excluding P. reclinata ($F_{3,7}$=7.75, p=0.004). Temperature explained 8.9% and river flow 16.7% of the total variance.

Comparisons with 1973-74

Distributions of fruit scores differed significantly between 1973-74 and 1988-89 for 5 of the 9 species examined. Acacia robusta, Pachystela msolo and Ficus sycomorus of Mnazini and Diospyros mespiliformes and Ficus natalensis of Mchelelo had significantly different distributions of fruit scores between 1973-74 and 1988-89 (Kolmogrov-Smirnov J'= 7, 9, 11, 7 and 7 for A. robusta, P. msolo, F. sycomorus, D. mespiliformes and F. natalensis, respectively, p<0.05). Acacia robusta had an extended fruiting season in 1973-74 relative to 1988-89 and Pachystela msolo had an extended fruiting season in 1988-89 relative to 1973-74. Diospyros mespiliformes, Ficus sycomorus and F. natalensis had more

uniform distributions of fruiting in 1973-74 than in 1988-89.

There were significant differences in monthly fruit scores between 1973-74 and 1988-89 for 3 of the 7 species in Mnazini and for 2 of the 6 species in Mchelelo. Ficus sycomorus and Acacia robusta in Mnazini received significantly higher mean monthly fruiting scores in 1973-74 than 1988-89 ($T=2.94$ and 2.75 for F. sycomorus and A. robusta, respectively, $p<0.05$), whereas individuals of Mimusops fruticosa received significantly higher fruiting scores in 1988-89 than 1973-74 ($T=2.28$, $p<0.05$). The same species in Mchelelo showed no significant differences in fruiting scores. Diospyros mespiliformes and the palm, Hyphaene compressa, had significantly higher mean fruiting scores in 1988-89 than 1973-74 in Mchelelo ($T=2.28$ and 2.28 for D. mespiliformes and H. compressa, respectively, $p<0.05$). Individuals of D. mespiliformes in Mnazini showed no significant differences in monthly fruiting scores between the 2 time periods.

Discussion

Mangabey foods were highly variable in their temporal abundance and spatial distribution. The majority of food species examined were rare and spatially clumped. Rarity and spatial aggregation are characteristic of many tropical tree species (Hubbel and Foster 1986, Robinson 1986, Struhsaker 1975) and may be the result of chance or particular

microhabitat requirements (Hubbel and Foster 1986). Hughes (1985) showed that several species occurring in the Tana River forests have very particular soil and water requirements for germination and growth. Because the frequency and depth of flooding, soil type and soil moisture holding capacity vary widely between forests and often within a single forest stand, different vegetative assemblages occur among forests and certain plant species may occur only in particular areas within a forest (Hughes 1985, Marsh 1978a, Homewood 1976).

The spatial distribution of mangabey food species should affect ranging behavior throughout the year, but because of the small size of the forests and the mangabeys' ability to traverse the entire area, spatial distribution should not affect whether the fruits of a particular tree species will be included in the diet. The relationship between plant abundance and temporal availability of fruits likely is more important. The abundance of a particular species limits the absolute availability of fruits to mangabeys; as plants become rarer, total fruit availability decreases and the amount of time when no fruits are available to mangabeys may increase.

Mangabey fruit resources show periods of relative abundance (November-May) and relative scarcity (June-October). The abundance of continuous, asynchronously fruiting species (e.g. Ficus sycomorus and Ficus

natalensis), however, can affect the temporal variation in fruit availability by dampening the severity of periods of scarcity. A critical number of individuals, however, is required to ensure that fruits are available each month. As these species decline in abundance, the probability that the species population has an individual bearing fruits during bottlenecks decreases. This is apparent in the monthly phenological scores for F. sycomorus individuals from Mnazini (n=7) and Mchelelo (n=10) forests (Fig. 12). Figs were unavailable during 3 months in Mnazini but at least 1 fig was fruiting in all months sampled in Mchelelo.

Species such as Phoenix reclinata and Diospyros mespiliformes that fruit at times when other species are not in fruit also can form important and critical food resources for mangabeys during months of otherwise low fruit production. The large fruit crop of P. reclinata, coupled with its extremely high density in the Mchelelo forest, resulted in abundant fruit during months of relative food scarcity in Nkano and Mnazini, forests with lower densities of reproductive palms (Fig. 13). The abundance of species such as P. reclinata and Ficus spp. may be a key factor in explaining the presence or absence of mangabeys in the various forest patches along the Tana River.

Many tropical forest species show adaptations toward fruit-drop and/or seed germination near the beginning of heavy rains (Rathche and Lacey 1985). Flowering occurs

primarily during periods of drought and low soil moisture (Ayres 1986, Monasterio and Sarmiento 1976, Croat 1975, Foster 1974, Koelmeyer 1960). This phenological pattern does not appear to prevail within the Tana River study sites. Although flowering occurs during times of low river water and rainfall, when soil moisture is low, there are few consistent associations between fruiting and environmental conditions. Fruit production by species that produce fruit continuously throughout the year, particularly Ficus spp., appear to be associated with the onset of the rains but the more seasonal species show no associations with rain. River flow and temperature also explained very little of the variance (25.6%) in a multiple regression model. It is likely that fruiting patterns of the Tana forests are influenced by a complex interaction of the variables examined here and perhaps more importantly, the position of the forest relative to the water table, the occurrence of floods, the depth and length of inundation during flooding and soil type. Fruiting time also may be more strongly correlated with elapsed time from germination than with environmental variables. Environmental cues seldom stimulate the onset of fruit ripening; onset is determined primarily by internal factors that control the rate of fruit development (e.g., production of sugars; Rathche and Lacey 1985).

Pronounced year-to-year variation in the onset and termination of the dry season could have important consequences for the flowering and fruiting phenologies of tree species (e.g. Chivers and Raemaekers 1980). The Tana riverine forests experience high year-round temperature with some seasonal variation, twice yearly rains and irregular flooding, with the severity and timing of rains and floods varying appreciably between years (Hughes 1985, Homewood 1976, Marsh 1976). The extreme unpredictability and annual variation in rainfall, temperature and flooding, overlaid with habitat degradation and fragmentation, make it difficult to determine causes of significant differences in fruiting patterns between 1973-74 and 1988-89. Wheelwright (1986) states that even 7 years of phenological data on species occurring in a Costa Rican montane forest, a habitat far less variable than the Tana River, were too few to determine supra-annual cycles of fruit production. The critical point however, is that total fruit availability will decline with decreasing abundances of reproductive trees. The abundances of several important food species (e.g. Ficus sycomorus, Ficus natalensis, Acacia robusta, Albizia glaberrima, and Mimusops fruticosa) declined between 1973-74 and 1988-89 in at least 1 or more of the study sites (Decker 1989, Medley 1990), effectively decreasing overall fruit production. Such long-term changes in the fruit

resource base may be shaping the present day feeding ecology of the Tana mangabey.

CHAPTER THREE

ACTIVITY PATTERNS AND DIET OF THE TANA RIVER CRESTED MANGABEY: EFFECTS OF SEASONAL AND LONG-TERM HABITAT CHANGE

Introduction

Comparisons of the proportion of time that animals spend on different activities are important in assessing inter- and intraspecific behavioral differences, and may be used to identify the adaptive nature of variability in temporal patterning of activities (Fa 1986). Variation in the ways in which animals partition time among different activities is seen in a wide range of primate species. Several generalizations have been made concerning the relationship between ecological factors and primate activity budgets (Clutton-Brock 1977, Crook and Gartlan 1966, Eisenberg et al. 1972, Robinson 1986, Struhsaker and Leland 1979). Diet and habitat structure have been shown to impose overwhelming constraints on animals use of time (Altmann, S. 1974). Because partitioning of time involves tradeoffs between metabolic requirements of different activities and the acquisition of energy to fulfill those requirements, diet quality and the temporal and spatial distribution of food strongly influence the amount of time spent in different activities (Oates 1986).

Monthly variation in activity budgets, particularly in the time spent feeding, has been demonstrated for several primate species and shown to covary with measures of food availability (e.g., Harrison 1985, Homewood 1976, Oates 1977, Robinson, 1986, Terborgh 1983, Waser 1975). In general, species relying heavily on foliage tend to decrease their level of activity during months when high-quality food is scarce, while species that rely heavily on fruits or insects increase the amount of time spent looking for and processing food during times of scarcity (Oates 1986). The spatial distribution of food also influences the amount of time individuals spend moving; individuals of species that feed on high density, evenly dispersed food spend less time moving than those of species that feed on widely dispersed food (Struhsaker 1980, 1978; Struhsaker and Leland 1979).

Optimal foraging theory predicts that an animal will act to maximize energy intake per unit time to meet demands for maintenance, movement, and reproduction (Stephens and Krebs 1986). Activity budgets therefore should reflect these actions. As the distribution and availability of food changes, time spent in energy-accruing behaviors (eating) versus more costly behaviors of searching for and moving between patches of food should change. The proportion of time spent in various activities forms a mutually dependent set, i.e., time spent in one activity affects the time available for other activities (Altmann and Altmann 1970).

Therefore, when animals must go through a long search or handling time per unit energy, major shifts in activity budgets will occur.

Although seasonal and daily variation in activity patterns are well documented for several primate species, very few studies have investigated long-term variation in activity budgets (Oates 1986). Furthermore, none has addressed the question of whether large-scale habitat change (e.g., forest loss and fragmentation) and subsequent change in the food resource base (e.g., lower resource availability), causes primates to reallocate time spent in different activities. The Tana River crested mangabey (Cercocebus galeritus) is an ideal species for addressing this question. Tana mangabeys have experienced severe habitat alteration over the last 15 years due to forest senescence, forest cutting for agriculture, and selective felling and pruning of species for building materials (Marsh 1986). These habitat changes, which involved the loss of important mangabey diet species, have resulted in an overall reduction in the food resource base.

In this paper, I examine the effects of these 15-year changes in the forest structure and food resource base on long-term variation in activity budgets. I also examine the temporal distribution (diurnal and seasonal) of activity patterns within and among 3 mangabey groups observed in 1988-89 and the influence of diet on time budgets. Finally,

I ask whether short-term associations between activity budgets and food resources are consistent with those observed after long-term habitat change.

Methods

Data Collection

I studied 2 groups of mangabeys in the Mchelelo forest and 1 group in the Nkano forest. Group size averaged 18 (range 13-19) and 28 (range 25-28) for the North and South Mchelelo groups, respectively, and 16 (range 12-17) for the Nkano group. Activity and diet data for 2 mangabey groups ranging in the Mchelelo and Nkano forests during 1973-74 were taken from Homewood (1976). Group size averaged 36 and 17 for these groups, respectively. Group age-sex composition did not differ significantly between the 2 studies ($G=8.4$, $df=5$, $p>0.05$). Although the 1973-74 Nkano group spent the majority of the observation months (66%) in an adjacent forest (Mnazini) 0.5 km south of Nkano, monthly activity budgets were not significantly different when the group ranged entirely in Nkano or Mnazini ($G=3.1$, $df=7$, $p>0.05$); I therefore used all monthly data for this group in the following analyses.

I collected data over 15 months on the Mchelelo groups (January 1988-March 1989) and 13 months on the Nkano group (March 1988-March 1989). Data were collected using methods similar to the previous study by Homewood (1976). I followed groups for 3 consecutive days each month from 0700 to 1830

hrs, with the exception of the S. Mchelelo group. This group frequently left the study site and was followed only while it was present in the Mchelelo forest. The group was observed for 3 consecutive days per month January 1988-April 1988 and November 1988; all other monthly samples consisted of non-consecutive 3-day samples or 1 or 2 day samples. No data were collected during May 1988 for either S. Mchelelo or Nkano nor during August 1988 for S. Mchelelo. The total number of contact hours for the 3 study groups was 595, 308 and 374 for N. Mchelelo, S. Mchelelo, and Nkano, respectively.

I sampled groups every half hour using a 10-minute scan (Altmann 1974, Robinson 1986), and recorded the following data for each individual located during a sample: 1) age; 2) sex; 3) identity; 4) height above the ground; 5) first activity sustained for 5 seconds; 6) species and item of food if eating (ripe or unripe fruit, ripe or unripe seed, flower bud or flower, shoots, stems and sprouts, leaves, gum, bark or dead wood, and animal prey); and 7) age, sex, and identity of the nearest neighbor within a 5 m radius.

I grouped activities into the same categories used by Homewood (1976):

1) Eating. This activity included animals ingesting or chewing food items. Animals scored as eating while moving were classified as eating.

2) Foraging. This category included both manipulatory and/or searching activity, excluding ingestion. Manipulatory foraging was any movement which involved manipulating a potential food object. Searching was defined as closely inspecting or sifting through leaf litter or foliage.

3) Moving. Movement included all locomotion except short movements during foraging, and locomotion during activities such as playing.

4) Inactive. This category included all stationary, nonsocial activity. Animals sleeping, sitting, lying, or standing were considered inactive.

5) Autogrooming. Any animal scratching or otherwise self-cleaning was autogrooming.

6) Allogrooming. Allogrooming included animals grooming or being groomed by another animal.

7) Social/Sexual. This was a composite category including: a) approach - individuals giving or receiving friendly or sexual presentations or embraces; b) aggression - individuals supplanting another from an occupied position, or lunging at, chasing or biting another, and individuals behaving submissively to another by posturing or retreating from a potential conflict; c) play - individuals engaged in mock-chasing or mock-fighting; d) sexual behaviors - mounting or copulating; e) maternal behaviors - nursing, picking up infant, etc.; and f) vocalizing - giving alarm calls and adult male long-calls.

Data Analysis

I estimated the amount of time spent in different activities by calculating the proportions of each activity recorded for all individuals during each day of a month, and taking the mean of the daily proportions. Data also were summarized by time-of-day by calculating the proportions of each activity recorded during each hour of the day in a given month and taking the mean of the hourly estimates. Mean hourly estimates were grouped into 3 time periods for analysis: morning (0700-1100 hrs.), mid-day (1100-1400 hrs.) and afternoon (1500-1800 hrs.). I further grouped data into 4 seasons: short rains (Nov-Jan), inter-rains (Feb), long rains (Mar-May), and dry season (Jun-Oct). Seasonal activity budgets were calculated by taking the mean of the appropriate monthly estimates. Finally, annual activity budgets were calculated by taking the mean of the all monthly estimates. This procedure corrects for the potential bias due to an unequal distribution of observation time among different months or hours of the day (Altmann and Altmann 1970).

I used analysis of variance methods (ANOVA, MANOVA) to simultaneously evaluate the effects of suites of independent variables on monthly activity budgets and diet composition (Neter et al. 1985). The use of MANOVA reduced the likelihood of Type I error resulting from multiple tests, and allowed simultaneous measurement of the effects of

independent variables (e.g., group, season, time-of-day) on correlated dependent variables (Sokal and Rohlf 1981). If MANOVA showed significant effect of independent variables on the suite of dependent variables, I then used ANOVA to examine the effects of these independent variables on each dependent variable. An arcsin square-root transformation was used on proportional data (Sokal and Rohlf 1981). I calculated significance values from partial sums of squares (Type III), which adjust each effect for all other effects in the model and are unrelated to cell frequencies (Freund and Littell 1981). When analysis of variance indicated significant differences due to an independent variable, I used least square means which adjust for unbalanced data, to determine where differences lay among the independent variables.

I used the same analysis of variance methods to compare activity budgets and diet composition between 1988-89 and 1973-74. I used G-tests (Sokal and Rohlf 1981) to test for differences in the distributions of social activities between 1988-89 and 1973-74 age-sex classes because repeated monthly samples were not available for the 1973-74 groups and only annual means were available.

Results

Variation in Activities 1988/1989

Mangabeys from all groups spent the majority of their time (58-64%) engaged in feeding behaviors (defined as

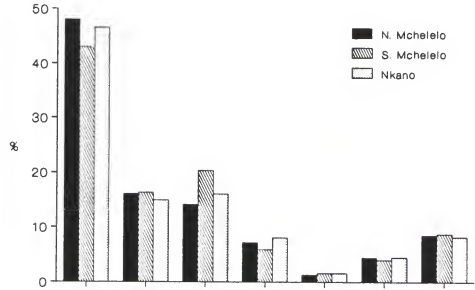
eating and foraging categories combined); social behaviors by comparison (social/sexual and grooming) occupied very little time (13-14%) (Figure 3.1, Table 3.1). There were significant negative correlations between proportion of time spent eating and a) inactivity ($r=-0.41$, $n=38$, $p<0.009$), b) moving ($r=-0.29$, $n=38$, $p<0.0001$), and c) foraging ($r=-0.43$, $n=38$, $p<0.007$), suggesting that time not devoted to eating was spent resting or traveling between and searching for food sources, but not necessarily socializing.

The proportion of time spent in each activity for all group members (excluding infants) varied among months and groups during 1988-89; the low standard errors, however, indicate little within month variation (Table 3.1). MANOVA showed highly significant effects of all independent variables and their interactions (group membership, season, and time-of-day) on the activity budget with the exception of the group by time-of-day interaction (Table 3.2). ANOVA showed group membership to have a significant effect on eating and inactivity (Table 3.3). Significant least squared means comparisons ($p<0.05$) showed that the N. Mchelelo group spent a higher proportion of time eating than either S. Mchelelo or Nkano, and Nkano was less active than either of the Mchelelo groups (Figure 3.1).

Seasonal differences were significant for foraging and social/sexual activities (ANOVA, Table 3.3). Foraging

Figure 3.1. Mean annual percent time spent among 7 behaviors by three 1988-89 mangabey groups and two 1973-74 mangabey groups.
a) 1988-89; b) 1973-74.

1988/89



1973/74

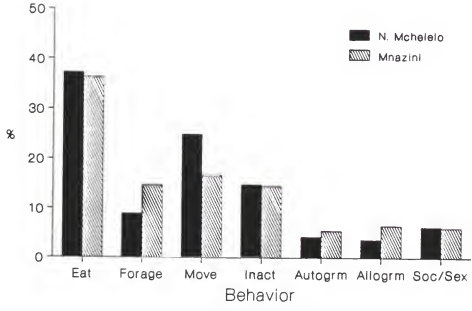


Table 3.1. Mean percent time spent in each activity by month for mangabeys in the 1988-89 N. Mchelelo, S. Mchelelo, and Nkano study groups. Standard errors are in parentheses. See text for definition of activities.

a) N. Mchelelo

Mon/Y	N(d)	Eat	Forage	Move	Inactive	Autogroom	Allogroom	Soc/Sex
Jan 88	3	50.9 (4.1)	13.9 (2.7)	20.7 (2.2)	4.5 (1.0)	0.5 (0.3)	2.8 (0.6)	6.6 (1.5)
Feb	3	52.7 (4.7)	18.1 (2.4)	13.9 (2.9)	4.0 (0.4)	1.3 (0.7)	4.2 (1.4)	5.1 (1.8)
Mar	3	43.5 (2.5)	19.1 (2.3)	19.3 (3.0)	4.6 (1.2)	0.8 (0.5)	6.2 (2.0)	5.4 (1.9)
Apr	3	54.6 (1.9)	12.5 (1.5)	16.5 (0.7)	8.4 (0.9)	0.9 (0.6)	2.4 (0.9)	4.4 (1.7)
May	3	42.4 (3.9)	21.8 (0.8)	12.8 (1.7)	8.7 (3.3)	0.7 (0.2)	5.5 (0.9)	7.5 (0.7)
Jun	3	52.3 (1.2)	14.8 (0.6)	16.6 (2.2)	5.5 (1.4)	0.7 (0.3)	4.3 (1.5)	4.9 (1.1)
Jul	3	48.7 (1.7)	18.2 (1.5)	13.1 (1.7)	8.7 (0.5)	1.6 (0.9)	3.0 (0.6)	6.6 (2.0)
Aug	3	46.6 (3.2)	17.0 (2.5)	13.2 (1.1)	9.8 (2.5)	1.4 (0.5)	4.2 (1.0)	7.1 (1.7)
Sep	3	44.1 (2.1)	21.6 (1.6)	11.9 (1.4)	8.2 (1.3)	0.7 (0.4)	7.1 (1.1)	6.0 (1.5)
Oct	3	42.7 (1.7)	19.6 (3.1)	15.2 (2.0)	7.2 (1.9)	1.2 (0.7)	4.3 (1.8)	9.7 (1.1)
Nov	3	49.8 (3.0)	8.9 (1.4)	10.2 (2.2)	8.1 (0.4)	1.7 (0.7)	5.2 (0.9)	15.7 (1.5)
Dec	3	48.2 (2.1)	11.1 (0.4)	14.2 (2.1)	5.2 (1.1)	3.3 (0.9)	4.1 (1.2)	13.7 (0.6)
Jan 89	3	46.9 (3.2)	15.1 (1.9)	10.6 (1.2)	8.8 (0.9)	1.3 (0.3)	3.8 (1.9)	12.7 (0.5)
Feb	3	53.0 (1.6)	13.3 (2.4)	12.9 (0.4)	4.8 (1.3)	1.3 (0.3)	4.8 (2.1)	9.4 (0.6)
Mar	3	44.6 (3.0)	16.0 (1.7)	9.8 (1.4)	9.6 (2.4)	1.9 (0.5)	4.2 (1.3)	12.9 (1.7)

b) S. Mchelelo

Jan 88	2	35.6 (5.2)	19.4 (1.6)	30.0 (2.9)	7.8 (2.9)	0.9 (0.3)	1.9 (1.9)	4.4 (0.6)
Feb	3	45.4 (4.6)	23.3 (2.3)	19.7 (6.5)	2.2 (1.1)	0.3 (0.2)	1.8 (0.9)	6.9 (2.7)
Mar	3	45.4 (3.9)	18.7 (0.4)	18.7 (0.6)	7.5 (2.0)	0.3 (0.2)	5.9 (1.2)	3.4 (1.7)
Apr	3	49.5 (1.7)	12.2 (1.2)	20.4 (2.3)	5.2 (1.8)	1.8 (0.6)	3.0 (1.0)	7.3 (1.3)
Jun	3	44.5 (4.4)	15.0 (1.9)	18.6 (4.2)	7.3 (1.4)	1.4 (0.2)	4.0 (1.4)	8.5 (1.3)
Jul	3	51.1 (6.4)	16.4 (2.6)	19.4 (2.7)	2.4 (1.5)	1.2 (0.2)	3.9 (0.8)	4.8 (1.4)
Sep	3	34.6 (1.4)	12.6 (1.9)	26.5 (2.3)	8.3 (0.7)	0.6 (0.3)	3.8 (0.9)	11.6 (0.4)
Oct	1	30.1 -	24.5 -	23.1 -	7.4 -	2.6 -	3.1 -	9.2 -
Nov	3	48.3 (1.2)	12.4 (1.0)	14.0 (0.9)	5.0 (0.3)	1.9 (0.1)	4.2 (0.4)	13.9 (0.6)
Dec	1	43.8 -	12.4 -	15.1 -	7.3 -	3.7 -	5.0 -	14.6 -
Jan 89	3	41.6 (1.7)	14.6 (1.9)	17.7 (5.1)	4.5 (2.5)	2.4 (0.7)	7.1 (1.9)	11.4 (0.8)

c) Nkano

Mar 88	3	46.5 (1.6)	17.0 (3.1)	16.5 (3.9)	6.4 (0.3)	1.7 (0.7)	6.7 (1.0)	5.1 (1.6)
Apr	3	42.3 (3.6)	13.6 (1.1)	22.4 (2.0)	9.4 (0.4)	1.4 (0.2)	4.4 (1.6)	6.4 (1.4)
Jun	3	45.6 (2.4)	18.0 (1.1)	20.1 (2.5)	6.1 (0.7)	2.0 (0.4)	2.0 (0.5)	6.1 (0.4)
Jul	3	46.4 (0.5)	16.1 (1.9)	19.7 (1.0)	8.0 (0.7)	0.7 (0.5)	4.1 (1.5)	4.7 (1.2)
Aug	1	50.31 -	15.9 -	11.5 -	7.0 -	1.3 -	3.2 -	10.0 -
Sep	3	52.4 (2.0)	14.6 (1.6)	17.3 (1.3)	4.2 (0.8)	1.3 (0.1)	4.5 (0.4)	5.5 (0.5)
Oct	3	45.7 (2.2)	13.8 (0.7)	19.3 (3.3)	7.3 (0.3)	1.2 (0.4)	6.3 (0.5)	6.0 (0.5)
Nov	3	58.7 (2.4)	9.0 (1.6)	10.8 (1.1)	7.2 (1.8)	1.2 (0.3)	2.4 (0.7)	10.5 (0.9)
Dec	3	40.4 (0.4)	9.8 (1.0)	13.1 (2.9)	10.4 (0.7)	2.5 (1.9)	6.7 (0.6)	16.4 (3.0)
Jan	3	35.7 (1.4)	17.4 (1.2)	16.4 (0.4)	13.3 (1.8)	1.2 (0.9)	4.8 (0.6)	11.2 (1.5)
Feb	3	45.4 (0.9)	15.5 (1.4)	14.4 (0.8)	10.4 (1.3)	2.8 (1.2)	3.1 (1.0)	8.1 (0.4)
Mar 89	3	48.3 (5.8)	17.4 (5.7)	10.1 (0.8)	6.8 (0.9)	2.2 (0.1)	5.5 (2.5)	9.2 (1.4)

Table 3.2. MANOVA results for group membership, season, and time-of-day differences among 1988-89 mangabey activity budgets.

Source	df	Wilks' Lambda	F-ratio	P
Group Membership	14	0.89	3.65	0.0001
Season	21	0.87	2.84	0.0001
Time-of-Day	14	0.83	6.23	0.0001
Group * Season	42	0.87	1.51	0.019
Group * Time-of-Day	28	0.93	1.08	0.343
Season * Time-of-Day	42	0.86	1.59	0.001

Table 3.3. ANOVA results for group membership, season, and time-of-day differences in 7 behaviors. Significance values are calculated from Type III partial sums of squares.

Source	df	Sum of Squares	Mean Squares	F	P
Eat					
Group	2	0.218	0.109	3.78	0.023
Season	3	0.096	0.032	1.11	0.345
Time-of-Day	2	0.037	0.018	0.64	0.529
Group * Season	6	0.191	0.032	1.10	0.359
Season * Time-of-Day	6	0.152	0.025	0.88	0.512
Error	441	12.715	0.029		
Forage					
Group	2	0.005	0.002	0.12	0.886
Season	3	0.383	0.128	6.29	0.0003
Time-of-Day	2	0.934	0.467	23.03	0.0001
Group * Season	6	0.193	0.322	1.58	0.149
Season * Time-of-Day	6	0.189	0.031	1.55	0.160
Error	441	8.948	0.020		
Move					
Group	2	0.139	0.069	2.68	0.069
Season	3	0.094	0.031	1.21	0.307
Time-of-Day	2	0.522	0.260	10.10	0.0001
Group * Season	6	0.111	0.019	0.72	0.635
Season * Time-of-Day	6	0.466	0.078	3.01	0.007
Error	441	11.382	0.026		
Inactive					
Group	2	0.316	0.158	6.63	0.002
Season	3	0.069	0.023	0.96	0.413
Time-of-Day	2	0.541	0.270	11.32	0.0001
Group * Season	6	0.380	0.063	2.65	0.015
Season * Time-of-Day	6	0.236	0.039	1.64	0.134
Error	441	10.536	0.024		
Autogroom					
Group	2	0.055	0.027	2.73	0.066
Season	3	0.274	0.009	0.91	0.437
Time-of-Day	2	0.053	0.026	2.63	0.073
Group * Season	6	0.133	0.022	2.21	0.041
Season * Time-of-Day	6	0.060	0.010	1.00	0.424
Error	441	4.434	0.010		

Table 3.3. -- Continued.

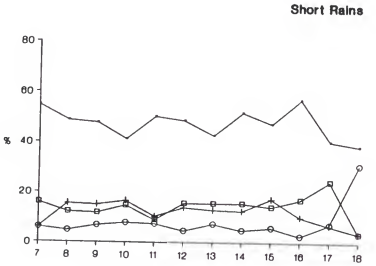
Source	df	Sum of Squares	Mean Squares	F	P
Allogroom					
Group	2	0.052	0.026	0.98	0.375
Season	3	0.086	0.029	1.08	0.356
Time-of-Day	2	0.183	0.092	3.44	0.033
Group * Season	6	0.107	0.018	0.67	0.676
Season * Time-of-Day	6	0.099	0.027	1.01	0.419
Error	441	11.730	0.026		
Social/Sexual					
Group	2	0.024	0.012	0.57	0.563
Season	3	0.659	0.220	10.61	0.0001
Time-of-Day	2	0.014	0.007	0.33	0.721
Group * Season	6	0.101	0.017	0.82	0.555
Season * Time-of-Day	6	0.106	0.018	0.85	0.529
Error	441	9.138	0.021		

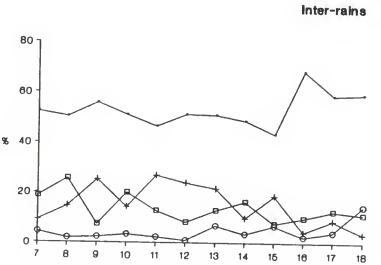
occupied a greater proportion of the activity budget during the drier seasons than the rainy seasons (Figures 3.2-3.4), and the groups were more social during the short rains than all other seasons of the year. Interactions between forest and season were significant for inactivity; the Nkano group spent a greater amount of time inactive during the inter-rains than either N. or S. Mchelelo.

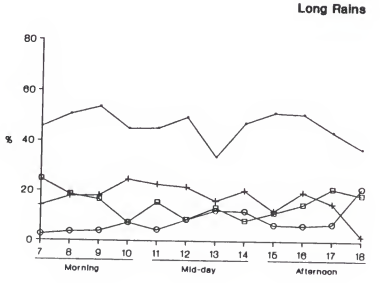
Time-of-day was significant for foraging, moving, inactivity and allogrooming (ANOVA, Table 3.3). On average, foraging occurred primarily during the morning (0700-1000) and mid-day hours (1100-1400), and groups became increasingly less active by the afternoon hours (1500-1800) when allogrooming increased (Figures 3.2-3.4). There also were significant interactions between season and time-of-day on moving. Groups moved more in the morning during the drier seasons, but showed a late-afternoon peak in movement during the rainy seasons (Figures 3.2-3.4).

In summary, there appear to be predictable hourly and seasonal patterns for certain activities. Although the 3 groups allocate differing amounts of time to various activities, they engage in similar activities during particular hours of the day. Mangabeys expend more of their daily activity budget in food gathering behaviors (e.g. foraging and moving) during drier seasons when food resources are less available, and engage more in social behaviors during the short rains when food resources are

Figure 3.2. Mean percent time spent in 4 major behaviors (eating, foraging, moving and inactive) by time-of-day and season for the 1988-89 N. Mchelelo group.


Short Rains
%
80
60
40
20
0
7 8 9 10 11 12 13 14 15 16 17 18


Inter-rains
%
80
60
40
20
0
7 8 9 10 11 12 13 14 15 16 17 18


Long Rains
%
80
60
40
20
0
7 8 9 10 11 12 13 14 15 16 17 18
Morning
Mid-day
Afternoon

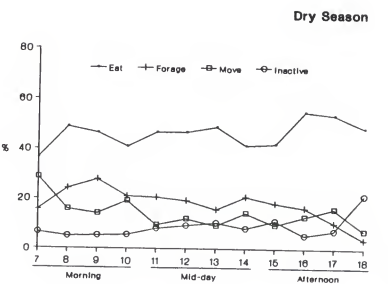
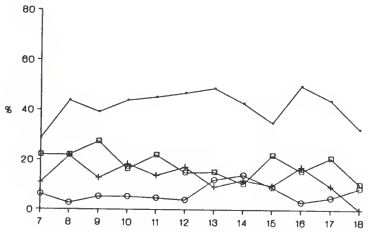
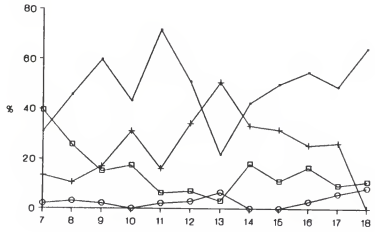

Dry Season
Eat
Forage
Move
Inactive
%
80
60
40
20
0
7 8 9 10 11 12 13 14 15 16 17 18
Morning
Mid-day
Afternoon

Figure 3.3. Mean percent time spent in 4 major behaviors (eating, foraging, moving and inactive) by time-of-day and season for the 1988-89 S. Mchelelo group.

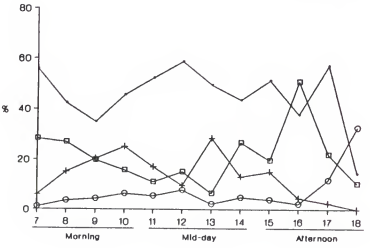
Short Rains



Inter-rains



Long Rains



Dry Season

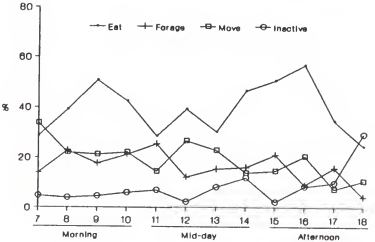
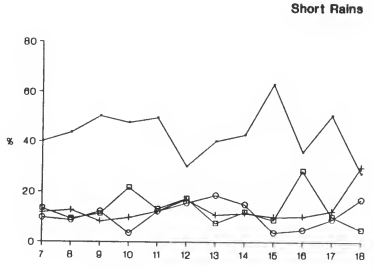
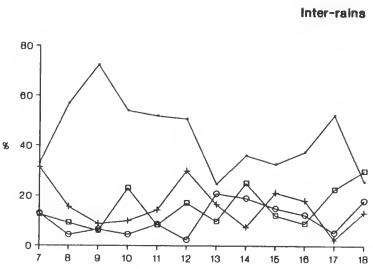
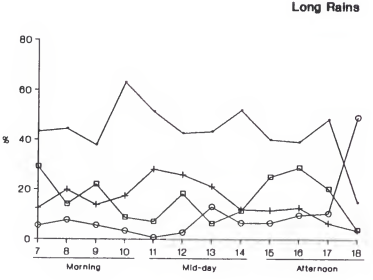
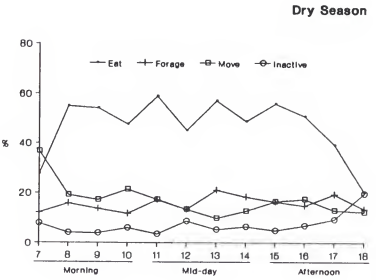


Figure 3.4. Mean percent time spent in 4 major behaviors (eating, foraging, moving and inactive) by time-of-day and season for the 1988-89 Nkano group.


Short Rains
%
80
60
40
20
0
7 8 9 10 11 12 13 14 15 16 17 18


Inter-rains
%
80
60
40
20
0
7 8 9 10 11 12 13 14 15 16 17 18


Long Rains
%
80
60
40
20
0
7 8 9 10 11 12 13 14 15 16 17 18
Morning
Mid-day
Afternoon


Dry Season
Eat
Forage
Move
Inactive
%
80
60
40
20
0
7 8 9 10 11 12 13 14 15 16 17 18
Morning
Mid-day
Afternoon

readily available (Chapter 2). Habitat and group size also may influence activity budgets. The Nkano group, which inhabits a larger forest with a richer resource base (Chapter 2), allocated more time to inactivity than either of the Mchelelo groups. The larger S. Mchelelo group ate less, was less active and moved more than either of the smaller groups.

Comparisons with 1973-74 Activity Budgets

Overall activity budget. MANOVA showed a significant effect of group (Wilks' Lambda=0.047, F=8.14, df=28,171, $p<0.0001$) on the overall activity budgets from two 1973-74 and three 1988-89 mangabey groups. One-way ANOVA showed significant group differences for all behaviors but social/sexual (F=10.4, 4.16, 7.69, 16.14, 23.72 and 4.59 for eating, foraging, moving, inactive, autogrooming, and allogrooming, respectively, df=4,53, $p<0.005$). Least square means comparisons showed that most of the significant differences ($p<0.05$) existed between the 1973-74 and 1988-89 groups, with fewer differences among groups of the same study. The 1973-74 groups ate less, were less active, and spent more time grooming than the 1988-89 groups (Figure 3.1). The differences between foraging and moving for the 5 groups were more complicated. The 1973-74 Mchelelo group moved more than all other groups with the exception of the 1988-89 S. Mchelelo group and foraged less than all other groups.

Social Behavior. I examined social behaviors more closely because the social/sexual category was a composite of rare but important behaviors, and 1973-74 social behavior data were available by age-sex class. I tested for differences in the 1973-74 and 1988-89 annual means for 7 social behaviors available for 1973-74 adult males, adult females, juvenile males, juvenile females, and male and female infants combined. These behaviors included: aggressing, aggressed, approaching, approached, allogrooming, allogroomed and playing. Because there were no significant interactions between groups and age-sex classes for grooming or social/sexual behaviors in 1988-89 (ANOVA, $p>0.3$), I combined data for my 3 groups and calculated annual means for social behaviors for each age-sex class.

There were no significant differences in the distribution of social behaviors between 1973-74 and 1988-89 for either adult males ($G=3.5$, $df=6$, $p>0.05$) or females ($G=5.9$, $df=6$, $p>0.05$, Figure 3.5). Differences exist, however, between the 2 studies for juvenile males ($G=21.5$, $df=7$, $p<0.005$), who spent a greater than expected amount of time playing in 1988-89 than 1973-74 ($G=9.9$, $df=1$, $p<0.005$) and juvenile females ($G=15.4$, $df=7$, $p<0.025$), who engaged in grooming more in 1973-74 than 1988-89 (Figure 3.6). There also was significant heterogeneity in the distributions of infant social behaviors between 1973-74 and 1988-89 ($G=68.7$, $df=5$, $p<0.001$). Infants of 1973-74 appeared to be more

Figure 3.5. Mean percent time spent in 7 social behaviors by 1973-74 and 1988-89 adult males and females. a) adult males; b) adult females.

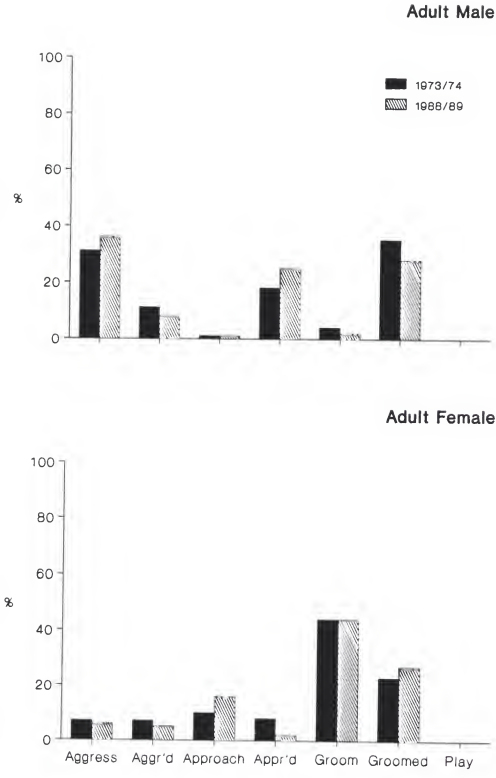
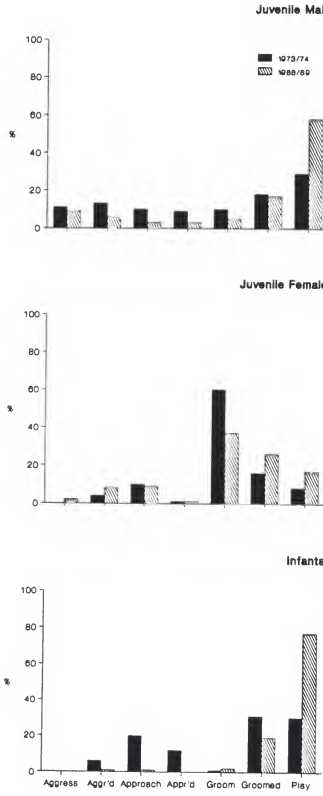

Adult Male
100
80
60
%
40
20
0
1973/74
1988/89
Adult Female
100
80
60
%
40
20
0
Aggress
Aggr'd
Approach
Appr'd
Groom
Groomed
Play

Figure 3.6. Mean percent time spent in 7 social behaviors by three age-sex classes in 1973-74 and 1988-89.
a) juvenile males; b) juvenile females; c) male and female infants combined.


Juvenile Male
1973/74
1988/89
%
100
80
60
40
20
0
Juvenile Female
%
100
80
60
40
20
0
Infants
%
100
80
60
40
20
0
Aggress
Aggr'd
Approach
Appr'd
Groom
Groomed
Play

involved in the overall social network of the group; they were the recipients of aggression and were involved in approaches significantly more than 1988-89 infants ($G=3.7$, 20.6 and 15.9 for aggressed, approach and approached, respectively, $df=1$, $p<0.05$), whereas 1988-89 infants stayed with their peer groups and played significantly more than the 1973-74 infants ($G=21.3$, $df=1$, $p<0.01$) (Figure 3.6).

Mother/infant associations. I addressed the question of whether the 1988-89 infants interacted less with group members and were weaned at a later stage than the 1973-74 infants by examining the patterns of mother/infant associations for the first 7 months of infancy. The percentages of time an infant a) clung to or nursed its mother, b) had its mother as its nearest neighbor, and c) was separated from its mother were compared for 5 infants from 1973-74 and 7 infants from 1988-89.

Infants were carried and suckled less, and associated with individuals other than their mother more as they aged (Figure 3.7, Table 3.4). Mother/infant associations and infant development, however, differed between the 2 study periods. The 1988-89 infants had their mothers as nearest neighbors more and associated with other group members less, particularly during the last 3 months of infancy, than 1973-74 infants (Figure 3.7). There were significant differences between studies in the amount of time infants spent clinging or suckling as they aged (Table 3.4, study*age interaction).

Figure 3.7. Percent time 1988-89 and 1973-74 infants spent in 3 levels of association with their mothers. Asterisks denote months when levels of association were significantly different between the 2 study periods.
a) Association A: the amount of time an infant was on its mother; b) Association B: the amount of time an infant had its mother as nearest neighbor; c) Association C: the amount of time infants were separate from their mothers.

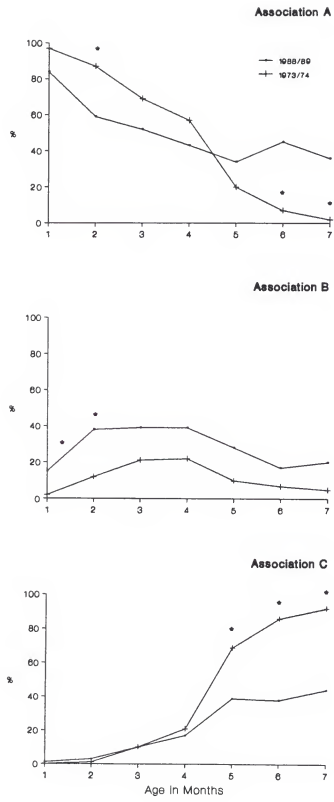

Association A
1988/89
1973/74
%
Association B
%
Association C
%
Age In Months

Table 3.4. ANOVA results for study (Homewood's 1973-74 study and the present 1988-89 study) and age differences in 3 measures of mother/infant association: a) amount of time infant is on its' mother, b) amount of time infant has mother as nearest neighbor and c) amount of time infant is separate from mother. Data were nested by infants within studies.

Source	df	Sum of Squares	Mean Squares	F	P
Association A					
Study[1]	1	0.009	0.009	0.07	0.793
Infant (Study)	10	1.227	0.123	2.78	0.007
Age	6	8.212	1.369	30.99	0.0001
Study * Age	6	2.172	0.362	8.20	0.0001
Error	59	2.606	0.044		
Association B					
Study[1]	1	1.043	1.043	16.77	0.002
Infant (Study)	10	0.622	1.043	33.25	0.0001
Age	6	1.277	0.213	6.78	0.0001
Study * Age	6	0.058	0.009	0.31	0.929
Error	59	1.852	0.031		
Association C					
Study[1]	1	0.759	0.759	7.97	0.018
Infant (Study)	10	0.952	0.952	2.44	0.017
Age	6	11.206	1.868	47.88	0.0001
Study * Age	6	1.519	0.253	6.49	0.0001
Error	59	2.301	0.390		

[1]F-statistic calculated using infant (study) as the mean-square error term.

Although 1988-89 infants were carried by their mothers less in the first months of infancy, they continued to cling and suckle in their sixth and seventh months, indicating that 1988-89 infants were weaned later than 1973-74 infants (Figure 3.7).

In summary, over a 15 year period, mangabeys appear to have made dramatic shifts in the allocation of time spent in various activities. The 1973-74 groups were, in general, less involved in feeding behaviors (eating and foraging) than the 1988-89 groups, and concomitantly spent more time in resting behaviors (grooming and inactive). Juveniles and infants showed the greatest differences in interactions with other group members. The 1988-89 juveniles and infants appeared to be less involved in the overall social network of their groups; juveniles reduced the amount of time grooming or increased the amount of time within the peer group, and infants associated more and longer with their mothers.

Diet

Diet composition. Of the combined eating observations for the 3 1988-89 groups, 6664 (73%) were plants, 887 (10%) were animals (primarily invertebrates); 1591 (17%) were unidentified items and 3 (<1%) were regurgitated matter. I observed mangabeys eating more than 58 different plant species during 107 observation days. The N. Mchelelo, S. Mchelelo and Nkano groups consumed 44, 36, and 31 of these

plant species over 45, 28, and 34 observation days, respectively (Appendix B). Although the number of plant species eaten varied monthly ($\bar{x}$=16.8 $\pm$ 3.76 for N. Mchelelo, $\bar{x}$=12.66 $\pm$ 3.44 for S. Mchelelo, and $\bar{x}$=16.25 $\pm$ 3.19 for Nkano), the top 5 diet plant species for each month constituted 72 to 100% of the feeding observations (Table 3.5). Thirteen plant species accounted for 59 of 75 (79%) potential top rankings in N. Mchelelo, 48 of 60 (80%) potential top rankings in S. Mchelelo, and 58 of 60 (97%) potential top rankings in Nkano (number of potential top rankings = 5 top rank positions * number of months in sample). Phoenix reclinata ranked in the top 5 species every month for at least 1 of the Mchelelo groups and in 9 of the 12 months sampled for Nkano. Either Ficus sycomorus or Saba comorensis ranked in the top 5 species of Nkano for 11 of the 12 months sampled. Thus, although mangabeys exploited a wide variety of foods, they concentrated feeding activity on a small number of plant species.

When the use of food items regardless of species was considered, fruit and seed contributed the most to the 1988-89 monthly diets (Tables 3.6 and 3.7, Figure 3.8). The majority of seeds eaten by each of the 1988-89 groups were unripe while fruits were consumed primarily in the ripe stage (Tables 3.6 and 3.7, Figure 3.8).

Table 3.5. Rank order of the five most common plant species eaten and the percentage of the total feeding records for identified plants (N) by group and month. Complete scientific names of plant species listed in Appendix B.

a) N. Mchelelo

	I		II		III		IV		V		
Month	Species	%	Species	%	Species	%	Species	%	Species	%	N
Jan 88	H. compressa	35	F. sycamorus	16	A. salviifolium	13	F. bubu	10	Grasses	8	134
Feb	H. compressa	34	P. reclinata	32	D. mespiliformes	8	O. spinosa	7	M. fruticosa	7	178
Mar	P. reclinata	35	S. madagascariensis	14	F. sycamorus	11	M. fruticosa	11	Grasses	9	207
Apr	P. reclinata	59	O. spinosa	10	S. madagascariensis	6	D. mespiliformes	5	Mushrooms	5	218
May	P. reclinata	61	O. spinosa	12	S. comorensis	6	H. compressa	5	A. venosum	4	172
Jun	P. reclinata	71	S. comorensis	8	O. spinosa	6	F. natalensis	5	D. mespiliformes	3	217
Jul	O. spinosa	18	D. mespiliformes	14	Mushrooms	14	P. reclinata	13	I. indica	11	168
Aug	P. reclinata	42	I. indica	18	H. compressa	11	D. mespiliformes	6	C. lukei	5	243
Sep	P. reclinata	43	I. indica	11	D. mespiliformes	11	H. compressa	8	C. lukei	8	196
Oct	P. reclinata	45	D. mespiliformes	9	O. spinosa	7	H. compressa	6	S. comorensis	6	164
Nov	A. paniculata	53	H. compressa	19	P. reclinata	6	O. spinosa	4	L. schweinfurthii	4	254
Dec	O. spinosa	27	L. schweinfurthii	26	F. sycamorus	11	Mushrooms	9	F. natalensis	7	229
Jan 89	P. reclinata	17	A. salviifolium	17	O. spinosa	11	H. zeylanica	9	P. msolo	8	241
Feb	F. natalensis	33	A. robusta	23	H. compressa	13	A. salviifolium	7	D. ferrea	6	273
Mar	P. reclinata	59	H. compressa	14	H. abyssinica	5	S. comorensis	4	C. rotundifolia	4	219

Table 3.5. -- Continued.

b) S. Mchelelo

Month	I Species	%	II Species	%	III Species	%	IV Species	%	V Species	%	N
Jan 88	M. compresse	44	P. reclinata	18	Q. spinosa	13	Grasses	10	M. fruticosa	5	62
Feb	M. fruticosa	37	M. compresse	19	P. reclinata	15	F. sycamorus	12	D. mespiliformes	5	155
Mar	P. reclinata	40	F. busei	19	S. madagascariensis	19	M. compressa	6	M. fruticosa	5	225
Apr	P. reclinata	49	C. goetzei	13	Grasses	9	F. natalensis	8	F. sycamorus	5	252
Jun	D. mespiliformes	27	P. reclinata	19	Mushrooms	15	S. comorensis	13	I. indica	5	144
Jul	P. reclinata	50	D. mespiliformes	14	M. compressa	11	Mushrooms	7	A. salviifolium	4	175
Sep	P. reclinata	61	I. indica	8	Grasses	8	Mushrooms	7	D. mespiliformes	4	107
Oct	P. reclinata	60	A. robusta	11	K. foetidissima	9	Q. spinosa	4	D. mespiliformes	4	45
Nov	A. paniculata	39	P. reclinata	27	M. compressa	8	Q. spinosa	6	S. comorensis	4	238
Dec	P. reclinata	31	Q. spinosa	26	F. natalensis	24	Mushrooms	11	G. livingstonei	8	55
Jan 89	A. salviifolium	32	Q. spinosa	13	P. reclinata	12	M. compressa	11	F. natalensis	8	181
Apr	P. reclinata	67	Mushrooms	11	K. foetidissima	6	A. venosum	4	Grasses	3	70

c) Nkano

Mar 88	F. sycamorus	47	P. reclinata	35	S. comorensis	4	P. msolo	4	Grasses	3	158
Apr	P. msolo	43	P. reclinata	25	F. sycamorus	15	S. comorensis	4	Grasses	4	172
Jun	S. comorensis	69	P. reclinata	11	P. msolo	9	Grasses	6	D. mespiliformes	3	126
Jul	S. comorensis	61	P. reclinata	13	Grasses	11	F. sycamorus	4	D. mespiliformes	3	151
Aug	P. reclinata	49	P. msolo	19	S. comorensis	12	Grasses	7	unknown vine	7	59
Sep	P. msolo	36	F. sycamorus	30	P. reclinata	30	S. comorensis	5	Mushrooms	1	203
Oct	P. multiflora	32	P. reclinata	27	S. comorensis	19	A. paniculata	11	F. sycamorus	4	170
Nov	A. paniculata	72	F. sycamorus	16	P. multiflora	3	S. comorensis	1	A. salviifolium	1	245
Dec	F. sycamorus	55	A. paniculata	24	A. salviifolium	12	Mushrooms	4	P. msolo	3	139
Jan 89	A. salviifolium	40	F. sycamorus	25	S. comorensis	14	P. msolo	7	A. paniculata	5	123
Feb	P. reclinata	53	S. comorensis	28	P. msolo	8	Q. spinosa	4	F. sycamorus	3	182
Mar	P. reclinata	43	S. comorensis	34	F. sycamorus	10	P. msolo	4	R. elliptica	3	190

Table 3.6. Percentage of diet items eaten by month and group. Unidentified items are not included.

a) N. Mchelelo

Month	Ripe Fruit	Unripe Fruit	Ripe Seeds	Unripe Seeds	Flowers	Leaves	Sprouts Shoots	Wood Bark	Gum	Animal	N
Jan 88	19.9	17.7	12.8	32.6	3.5	0.0	11.3	0.0	0.0	10.6	141
Feb	13.9	1.0	7.5	59.7	5.5	2.5	2.5	0.0	0.0	7.5	201
Mar	26.9	0.0	1.4	34.4	0.5	0.5	9.9	0.9	0.0	14.6	212
Apr	13.9	6.8	0.7	50.7	0.4	0.7	1.4	1.1	0.0	24.3	280
May	24.6	27.2	2.1	22.1	4.6	1.5	1.5	6.6	0.5	9.2	195
Jun	15.4	5.8	1.2	59.8	0.0	0.4	1.5	1.2	0.0	14.7	259
Jul	21.3	14.9	18.4	9.2	0.0	2.3	14.4	4.6	0.0	14.9	174
Aug	20.6	27.2	1.2	40.5	1.6	1.2	1.2	1.2	2.3	3.1	257
Sep	30.6	14.8	6.2	31.6	2.9	2.9	2.9	0.5	0.5	7.2	209
Oct	22.2	6.2	19.6	24.7	7.2	1.0	1.0	4.1	2.1	11.8	194
Nov	10.9	0.4	53.8	21.5	1.1	0.0	0.4	1.8	2.5	7.6	275
Dec	62.8	10.6	9.7	5.3	0.0	1.3	1.3	0.4	0.0	8.4	226
Jan 89	43.7	8.3	2.0	9.9	15.1	2.8	5.2	2.0	0.8	10.3	252
Feb	38.1	5.8	2.7	27.1	4.6	2.1	0.6	1.8	2.4	14.6	328
Mar	6.1	3.4	10.9	51.9	2.7	3.4	1.5	6.1	0.0	14.0	264

b) S. Mchelelo

Jan 88	21.5	7.7	12.3	41.5	0.0	4.6	10.8	0.0	0.0	1.5	65
Feb	39.5	3.7	3.7	23.7	6.3	0.5	3.7	1.0	0.0	17.9	190
Mar	11.7	19.9	1.1	47.5	0.0	1.9	3.0	2.6	0.0	12.1	265
Apr	7.0	10.2	2.9	57.0	2.2	0.4	6.3	5.1	0.0	8.8	272
Jun	14.7	9.0	7.1	34.6	1.3	2.6	4.5	3.8	0.0	22.4	156
Jul	20.2	4.0	5.8	54.9	0.6	1.2	6.4	2.9	0.0	4.0	173
Sep	44.7	9.7	0.0	28.2	0.9	0.0	7.8	6.8	0.0	1.9	103
Oct	11.7	9.8	29.4	21.6	0.0	5.9	1.9	0.0	7.8	11.8	51
Nov	3.9	3.9	68.4	9.1	0.9	0.0	1.7	0.9	0.0	10.4	231
Dec	49.2	1.5	22.4	4.5	0.0	0.0	0.0	1.5	0.0	20.9	67
Jan 89	50.3	4.6	2.6	10.8	12.3	0.5	9.7	3.6	0.0	5.6	195

Table 3.6. -- Continued.

c) Nkano

Month	Ripe Fruits	Unripe Fruits	Ripe Seeds	Unripe Seeds	Flowers	Leaves	Sprouts Shoots	Wood Bark	Gum	Animal	N
Mar 88	37.2	5.2	2.1	29.7	4.2	1.6	2.6	3.7	0.0	13.6	191
Apr	45.6	12.3	0.0	23.6	0.0	1.5	3.1	2.1	0.0	11.8	195
Jun	53.5	2.9	0.6	7.6	0.0	1.2	6.4	2.9	0.0	25.0	172
Jul	43.1	2.5	13.7	4.1	0.0	1.5	8.6	8.1	0.0	18.3	197
Aug	4.5	3.0	0.0	43.3	25.4	3.0	6.0	6.0	0.0	9.0	67
Sep	19.5	8.8	0.0	31.2	34.4	0.0	0.0	0.0	0.0	6.0	215
Oct	31.2	5.8	12.6	35.5	1.1	1.1	1.1	2.2	1.1	9.0	189
Nov	10.1	9.0	66.0	0.0	1.1	0.0	0.7	5.2	0.0	7.8	268
Dec	58.1	1.3	0.6	0.6	0.0	0.6	21.9	3.9	0.0	12.9	155
Jan 89	45.3	11.3	0.6	5.7	0.6	0.6	8.2	6.3	0.0	21.4	159
Feb	3.3	2.8	0.0	67.0	5.6	1.4	2.3	4.2	0.0	13.5	215
Mar	8.4	5.3	0.0	64.2	3.5	0.9	2.2	1.8	0.0	10.2	226

Table 3.7. Frequency of plant parts eaten for common diet species of the 3 study groups.

a) N. Mchelelo

Species	Ripe Fruits	Unripe Fruits	Ripe Seeds	Unripe Seeds	Flowers	Leaves	Sprouts Shoots	Wood Bark	Gum	Total
Phoenix reclinata	29	50	83	761	53	1	12	23	0	1012
Hyphaene compressa	49	9	24	230	4	0	0	0	0	322
Oncoba spinosa	239	10	0	0	0	0	0	1	0	251
Aporrhiza paniculata	0	0	134	0	0	0	5	1	0	140
Ficus natalensis	124	4	0	0	0	0	0	0	0	128
Diospyros mespiliformes	59	0	10	43	0	0	1	0	0	113
Alangium salviifolium	73	0	5	2	1	0	21	2	0	104
Acacia robusta	0	0	5	65	0	2	0	0	29	101
Tamarindus indica	14	82	0	0	0	0	0	0	0	96
Ficus sycamorus	37	53	0	0	0	0	0	0	0	90
Lannea schweinfurthii	54	0	8	11	0	0	0	0	0	73
Saba comorensis	19	18	0	7	4	4	0	2	0	54
Sorindeia madagascariensis	10	30	3	0	0	5	0	0	0	49

b) S. Mchelelo

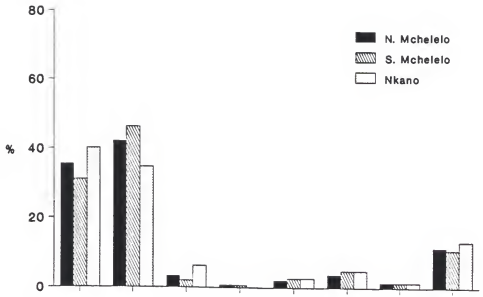
Phoenix reclinata	47	3	106	390	30	2	6	18	0	602
Hyphaene compressa	32	0	9	96	0	0	0	0	0	137
Aporrhiza paniculata	0	0	93	0	0	0	1	0	0	94
Diospyros mespiliformes	18	2	5	58	0	0	0	2	0	85
Alangium salviifolium	57	0	5	1	0	0	11	1	0	75
Mimusops fruitcosa	72	0	0	1	0	0	0	0	0	73
Oncoba spinosa	66	3	0	0	0	0	0	0	0	69
Ficus bussei	11	27	0	5	0	0	0	0	0	43
Cordia goetzei	0	0	0	33	0	0	0	0	0	33
Tamarindus indica	0	18	0	3	1	0	0	0	0	22
Acacia robusta	0	1	1	0	0	0	0	0	4	6

c) Nkano

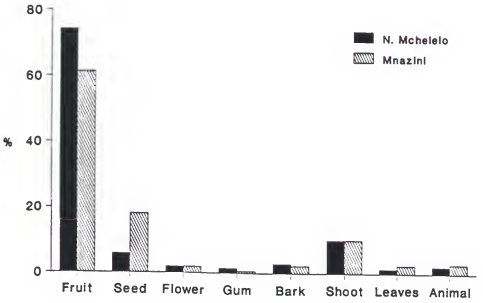
Phoenix reclinata	2	1	40	389	8	0	4	3		447
Saba comorensis	169	0	2	165	5	11	3	22		377
Ficus sycamorus	247	94	0	0	0	1	0	2		342
Aporrhiza paniculata	0	4	175	14	0	0	39	1		233
Pachystela msolo	88	6	2	7	96	1	4	15		219
Alangium salviifolium	63	0	3	1	1	0	8	2		78
Polyspheeria multiflora	61	2	0	0	0	0	0	0		63

Figure 3.8. Percent composition of diet by item for 1973-74 and 1988-89.
a) 1988-89; b) 1973-74.

1988/89



1973/74



Associations between activity budget and diet. Monthly activity budgets varied with diet composition and food availability. The amount of time spent feeding (eating + foraging) for the 3 1988-89 groups was negatively correlated with percent ripe fruit in the diet ($r=-0.48$, $n=38$, $p<0.002$) and was positively correlated with percent unripe seed in the diet ($r=0.36$, $n=38$, $p<0.02$). When eating and foraging were treated separately, eating, but not foraging, was negatively correlated with the amount of fruit in the diet ($r=-0.40$, $n=38$, $p<0.01$). There were no significant associations between foods other than fruit in the diet (e.g. invertebrates) and amount of time spent in the different activities. Although levels of inactivity showed no relationships with diet, inactivity was strongly correlated with feeding ($r=-0.49$, $n=38$, $p<0.002$); as the amount of time spent foraging and eating decreased, levels of inactivity increased. Plant species dietary diversity (Shannon-Weiner H', Pielou 1969) also was negatively correlated ($r=-0.49$, $n=30$, $p<0.005$) with measures of fruit availability (see Chapter 2), particularly ripe fruit. Thus, as fruit resources became scarce, the diet broadened and the amount of time spent in feeding behaviors increased.

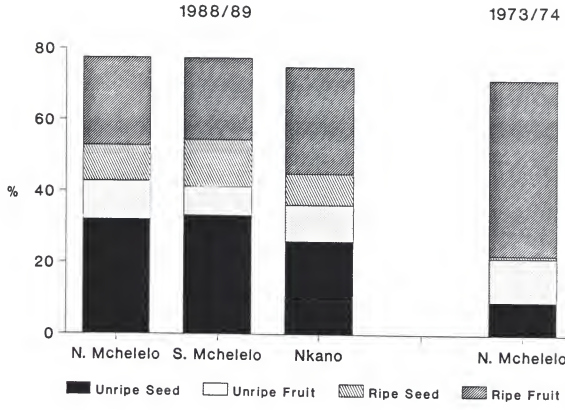
Comparison with 1973-74 diet composition. The contribution of fruit, seed and other items to the diet differed between 1973-74 and 1988-89 (Figure 3.8). MANOVA showed a highly significant effect of group on the overall

diet composition (Wilks' Lambda=0.28, df=16,153, F=4.95, p<0.0001). There were significant group differences in the representation of fruit (1-way ANOVA, F=7.24, df=4,53, p<0.001), seed (F=6.99, df=4,53, p<0.001) and invertebrates (F=15.74, df=4,53, p<0.001) in the diet. Significant least square means comparisons (p<0.05) showed that the 1988-89 groups consumed fewer fruits and greater numbers of seeds and invertebrates than the 1973-74 groups (Figure 3.8).

Data on consumption of ripe versus unripe fruits and seeds for one 1973-74 Mchelelo group suggested that the 1988-89 groups consumed less ripe and more unripe fruits and seeds than the 1973-74 group (Figure 3.9). MANOVA showed a significant effect of group on the amount of ripe and unripe fruits and seeds in the diet (Wilks Lambda=0.68, F=3.25, df=6,92, p<0.006). The 1973-74 group had a significantly higher intake of ripe material (F=5.03, df=3,47, p<0.004) and a significantly lower intake of unripe material (F=4.69, df=3,47, p<0.006) than the 1988-89 groups. The differences in the intake of ripe and unripe material were due primarily to an increase in unripe seed consumption (F=5.06, df=3,p<0.004) and, to a lesser degree, a decrease in ripe fruit pulp consumption by the 1988-89 groups (Figure 3.9).

Measures of diet diversity were similar between the 1988-89 and 1973-74 Mchelelo groups. Mean monthly diet diversity for the 1973-74 Mchelelo group (H'=1.90) did not differ significantly from H' for either the 1988-89 N.

Figure 3.9. Percent ripe and unripe fruit and seed items in the diet.
a) for three 1988-89 mangabey groups; b) for 2 1973-74 mangabey groups.


1988/89
1973/74
80
60
%
40
20
0
N. Mchelelo
S. Mchelelo
Nkano
N. Mchelelo
Unripe Seed
Unripe Fruit
Ripe Seed
Ripe Fruit

Mchelelo (H'= 1.89, t=-0.24, df=18, p>0.8) or the S. Mchelelo H'=1.95, t=0.16, df=11, p>0.8) group. Mean monthly diet diversity, however, decreased significantly between 1973-74 and 1988-89 for the Nkano group (H'=1.40, 1988-89 and H'=2.12, 1973-74, t=6.04, df=21, p<0.0001).

In summary, differences in activity budgets and diet among the 1988-89 groups were similar to differences in behavior and diet observed between the 1973-74 and 1988-89 study periods. There was an association between increased feeding time and decreased fruit availability both within and between studies. As ripe fruit and seed in the diet decreased within and between years, the amount of time spent in feeding behaviors also increased. Increased time spent in feeding behaviors, concomitantly decreased the amount of time available for grooming and inactivity both among the 1988-89 study groups and between the 1988-89 and 1973-74 studies. The only inconsistent association was between diet diversity and fruit availability; 1988-89 diet diversity did not increase with decreased fruit availability, and mean monthly diet diversity for Nkano was lower in 1988-89 than 1973-74.

Discussion

Many studies have shown that feeding behaviors take precedence over social or other activities, particularly for species such as mangabeys (Waser 1975), baboons (Altmann 1974, Post 1981), and macaques (Fa 1986) that concentrate on

widely dispersed, temporally fluctuating food resources. The inverse association found between eating and other behaviors in the Tana mangabey is consistent with that shown for a wide range of primate species feeding primarily on fruits (Clutton-Brock and Harvey 1977, Struhsaker 1978, 1980). Because fruits are less evenly distributed and relatively more unpredictable than foliage (Waser 1976), species relying primarily on fruits must invest more time searching for food resources. Primates eating primarily fruits also do not require the extended periods of rest needed for digestion of foliage. The greater digestion rate in primarily frugivorous species relative to folivorous species (Clemons and Phillips 1980, Milton 1981) requires a faster and/or more consistent input of food to achieve adequate nutritional intake; this results in a greater amount of the daily activity budget invested in eating (Clutton-Brock and Harvey 1977).

Predictable temporal variability in mangabey activity patterns occurred on a daily and seasonal basis. The biphasic or triphasic patterns of activities typical of most primates (Fa 1986, Post 1981) however, were not marked in the Tana mangabey. Most behaviors, with the exception of grooming and inactivity, peaked in the cooler, early morning hours, particularly during the dry season. Eating occupied a relatively constant proportion of the daylight hours with the exception of approximately an hour in the early morning

and late afternoon. The Tana mangabeys' temporal pattern of activities is more consistent with that observed for large-bodied, terrestrial primates. Several species of savanna baboons display a less marked diurnal variation with feeding, in particular, occupying a relatively constant proportion of the daily activity budget (Papio anubis: Aldrich-Blake et al. 1971, Nagel 1973, Harding 1976, Rose 1977; Papio cynocephalus: Post 1981; Papio ursinus: Davidge 1978, Hall 1962; Theripithecus gelada: Crook and Aldrich-Blake 1968, Dunbar and Dunbar 1974, Iwamoto 1975). This may be due to the poorer quality diets of these species and the need to feed more consistently throughout the day, and/or their use of multiple diet items, each requiring different handling and search times.

Although daily variability in activity patterns may be influenced by climatic conditions such as temperature and rainfall (Bernstein 1976, Marsh 1978b, 1981a) or "scheduled activities" (sensu Altmann 1974) such as the necessity to climb into sleeping trees before dark, seasonal variability in activity budgets more likely is affected by changes in food availability than climatic variation per se (Clutton-Brock 1974). Post (1981) and Clutton-Brock (1974) found no correlation between activity and climate for the yellow baboon (Papio cynocephalus) and red colobus (Colobus badius), respectively and both implicated seasonal changes in food resources. Although Marsh (1978b) found a

correlation between activity and daily temperature for the Tana River red colobus (Colobus badius rufomitratus), seasonal changes in food availability also influenced activity. Tana mangabeys expended more of their daily activity budgets foraging during drier seasons when food resources were less available and more widely dispersed (Chapter 2). Conversely, when food resources were more readily available, particularly during the seasonal short-rains, mangabeys spent more time in social/sexual activities.

Group differences in activity budgets also may be related to gross habitat differences. The Nkano group was less active, particularly during the inter-rains, than the Mchelelo groups. The Nkano group, although ranging in a less diverse forest than the Mchelelo groups, had access to a potentially richer resource base that was more evenly distributed throughout the year (Chapter 2). The richer, more reliable resource base may have enabled the Nkano group to allocate more time to inactivity. Group size also may have played an important role in the distribution of activities. The N. Mchelelo and Nkano groups were similar in size and activity budgets. The larger S. Mchelelo group, in general, ate less, moved more, and was less active than the 2 smaller groups.

Despite the complexities of inter-study comparisons (Altmann 1974, Clutton-Brock 1977), the strong contrast

between 1973-74 and 1988-89 activity budgets may not be due to sampling bias alone. Intergroup variability was low or insignificant in both the 1973-74 and 1988-89 studies, and differences between the 2 studies were highly significant. Inter-study differences may have been the result of changes in the forest habitats over the 15-year period or differences in behavioral scoring by Homewood and myself. Although the latter possibility was not tested and may play a role in the observed behavioral changes, inter-study differences in behaviors that were less likely to be confused or scored differently by separate observers (e.g., resting, grooming, and suckling) were significant and increases confidence in the comparisons.

The 1988-89 mangabey groups spent significantly more time eating and searching for food and less time grooming and inactive than the 1973-74 groups. These results are similar to those reported for Japanese monkeys (Macaca fuscata) in habitats of deteriorating quality (Nakagawa 1989) and are consistent with 1988-89 trends between activity budgets and variation in habitat quality due to seasonal and forest differences.

Increased search time in 1988-89 was expressed through increased time spent foraging, but not through increased movement (with the exception of the S. Mchelelo group that underwent long movements between 2 forest patches). Based on optimal foraging theory (Charnov 1976), mangabeys should

spend more time exploiting a fruiting tree and less time traveling between trees as the probability of encountering a fruiting tree or a tree in the preferred phenological state declines. The cost of leaving a fruiting tree and moving to another increases as trees become rarer and farther apart. Mangabeys made direct inter-patch movements only when several large trees of 1 or 2 widely dispersed species (e.g., Ficus spp.) were fruiting synchronously; otherwise they made slow, non-direct movements. Slow inter-patch movement, during which mangabeys continuously foraged for seeds and invertebrates on the forest floor, should have minimized the cost of travel and maximized food intake.

Once food was encountered, the 1988-89 mangabeys spent more time eating than 1973-74 mangabeys. Increased time spent eating in 1988-89 may have resulted from greater handling times of common diet items or an actual increase in intake to compensate for lower diet quality. Although feeding rates are not available for the 2 studies, the overwhelming dependence on Phoenix reclinata fruits in 1988-89 would have lowered, not increased, handling times. Phoenix reclinata fruits are small and grow in easily harvested clusters. Handling time is brief even when mangabeys are selectively feeding on unripe seeds, and the small fruit size allows mangabeys to fill their cheek pouches and continue foraging for other food items while processing palm fruits.

Studies on captive and provisioned versus free-ranging Barbary macaques (Macaca sylvanus) have shown that food quality strongly influences activity budgets; macaques provisioned with high quality foods spend significantly less time eating and more time inactive than their free-ranging counterparts (Fa 1986). The switch by 1988-89 groups to primarily unripe seed and fruit may have resulted in a lower quality diet. Ripe fruits, because of their concentration of nutrients and readily metabolized simple sugars, offer an outstanding source of available energy (Waterman 1984). Unripe seed and fruits are less desirable energetically and high levels of secondary metabolites present in unripe seeds and fruits further reduce diet quality. Secondary metabolites such as tannins, that inhibit digestion or alkaloids that interfere with specific physiological processes, have been shown to be higher in unripe verses ripe fruits (Gartlan et al. 1980). The fact that unripe fleshy fruits are more likely to contain inhibitory secondary metabolites than other fruit types (McKey et al. 1981) may explain why mangabeys rarely consumed unripe fleshy fruits (e.g., Ficus spp.) and fed primarily on non-fleshy fruits or seeds in the unripe stage (Table 3.7).

Diet composition may result from a critical balance between nutrient content and tannin/alkaloid content of food items, such that food items become unattractive when a certain cost/benefit ratio is exceeded (Gartlan et al. 1980,

Davies et al. 1988). Seeds may have a lower cost/benefit ratio because they are rich protein sources and, relative to other plant items, have fewer digestion-inhibitors (McKey et al. 1981, Waterman 1984). Although toxic fatty acids and alkaloids are present in unripe seeds, most tannins are found in easily discarded seed coats (McKey 1979, Waterman 1984). Perhaps, mangabeys as monogastric primates, are not as adept at dealing with secondary compounds as the folivorous Colobine monkeys. A shift to unripe seeds and other starch- or protein-rich diet items such as invertebrates (even with the added cost of increased foraging time) may constitute the best alternative strategy when ripe fruits are unavailable. Berenstain (1986) showed a similar diet shift from primarily ripe fruits and seeds to unripe seeds and insects by long-tailed macaques (Macaca fascicularis) in Borneo after a severe fire when ripe fruits were unavailable.

The lower availability of ripe fruits to mangabeys in 1988-89 may have been due both to reduced numbers of fruiting trees by habitat loss or increased competition for ripe fruits with yellow baboons. Fruit abortion and frugivory generally results in unripe fruits being consistently more abundant than ripe fruits. Many species fruit asynchronously (e.g. Ficus spp.), both within and between individuals; a reduction in the total number of individuals in a given population, therefore, will reduce

the probability of finding another individual not only in fruit, but bearing ripe fruits. More synchronously ripening species (e.g. Garcinia livingstonei and Phoenix reclinata) that offered rich sources of ripe fruits often were unavailable to mangabeys because of competition with yellow baboons. Baboons, in groups of more than 80 individuals, were always successful in supplanting mangabeys from contested food patches. Mangabeys therefore may have been unable to wait for preferred ripe fruit items and switched to more abundant and less contested diet items.

Diet quality and consequent shifts in activity budgets may influence infant dependency and schedules of development. Silk and Kraemer (1978) showed that chimpanzee mother/infant associations were influenced by environmental conditions. Infants gained independence more quickly among captive, provisioned chimps than their wild counterparts. Mangabey infants in 1988-89 associated with their mothers for longer and were weaned at a later age than 1973-74 infants. If the opportunity for an infant to move away from its mother and interact with other group members is greater when a mother is inactive, then the more mobile 1988-89 mothers may have limited those opportunities. Struhsaker (1980) found that red colobus (Colobus badius) infants played more than infant redtail monkeys (Cercopithecus ascanius), and speculated that the more stationary red

colobus mothers provided their infants with a greater opportunity to play.

A reduction in the overall food supply, and/or a shift to less nutritious food items also may have increased the length of dependency on the mother if a) the mother had a decreased milk production or b) an inexperienced, infant forager was unable to locate or compete for food resources. Extended infant dependency should delay the incorporation of juveniles into the social network of the group. Juveniles therefore might be expected to spend more time with peers than with older group members (O'Brien 1990, Walters 1986); this may be supported by the great amount of time 1988-89 juvenile males spent playing. Increased play, however, would not be expected during times of nutritional stress. Baldwin and Baldwin (1971) and Lee (1984) show reduced play in squirrel monkeys (Saimiri spp.) and vervets (Cercopithecus aethiops), respectively, in less productive habitats and during times of reduced food supply. Differences in estimates of play by 1988-89 and 1973-74 juvenile male mangabeys may be more a function of group demography than nutritional status. The juvenile sex ratio in 1988-89 was 8 males: 5 females versus 1 male: 4 females in 1973-74 (Homewood 1976). Because juvenile male mangabeys play more than any other age/sex class (Homewood 1976), the differences in sex ratio could have effected rates of play.

Homewood (1978) described the Tana mangabey as a highly adaptable, flexible primate that could adjust its behavior to buffer fluctuations in resource availability in a highly seasonal habitat. My results corroborate this and further suggest that the mangabeys' behavioral and dietary flexibility has enabled it to adapt to large-scale habitat change. Such adaptability may enhance the mangabeys' chances for long-term persistence. Both the mangabey and the sympatric Tana River red colobus monkey (Colobus badius rufomitratus) experienced population declines between 1976 and 1985. The mangabey, although initially the rarer species, declined less and is now found in greater numbers (680-725 individuals, Chapter 6) than the more specialized, folivorous red colobus (200-300 individuals, Decker 1989). The mangabeys' greater resilience may have been due to its more opportunistic diet and greater ability to adjust to habitat change than the red colobus (Decker and Kinnaird 1990, Marsh 1986).

Why should such an adaptable monkey be so rare and endangered? The rarity of all 4 subspecies of Cercocebus galeritus may be attributed, in part, to habitat requirements. Homewood (1978) speculated that because of their semi-terrestriality and flexible foraging and social behaviors, C. galeritus subspecies are well suited to exploit temporary superabundances of fruit, dense sub-canopies and frequently flooded terrain. She speculated

further that they may be less competitive in higher stature or more open forests than other primates (e.g., guenons and baboons) that are better suited for a more arboreal or terrestrial lifestyle and rely to a greater extent on more readily available and/or lower-energy foods. That yellow baboons and Sykes monkeys (Cercopithecus mitis) have not declined along the Tana River supports the idea that C. galeritus is more affected by competition.

The Tana mangabeys' endangered status is primarily the result of the highly restricted distribution of Tana forest habitat and the rapid destruction of this habitat. Forest patch size and degree of isolation may influence the presence or persistence of mangabey groups (Chapter 5). Small patches may not contain enough individuals of rare diet species (e.g., Ficus spp.) or extensive enough stands of stable food items (e.g., Phoenix reclinata) to support groups of mangabeys. Isolation of patches also may limit opportunities for colonization or recolonization of formerly occupied forests; mangabeys readily cross open woodland, but they have never been observed crossing extensive grasslands or non-forested distances greater than 0.5 km.

CHAPTER FOUR

COMPETING USES OF A FOREST PALM, Phoenix reclinata N.J. JACQUIN, BY HUMANS AND TANA RIVER CRESTED MANGABEYS

Introduction

Non-destructive, sustained-yield harvesting of plant and animal resources by rural people could play an important role in tropical forest conservation (e.g., Myers 1984, Peters et al. 1989, Vasquez and Gentry 1989). Regulated harvesting may have minimal impacts on tropical forests while generating substantial economic returns to rural people, thereby providing alternatives to more destructive types of land use. Peters et al. (1989), for example, show that market-oriented extraction of fruits by villagers from some Amazonian forests provides a promising, economic alternative to deforestation. Other field workers however, have illustrated the potential negative aspects of such an economy. Redford and Robinson (1987) and others (Smythe 1978, Mittermeier in press) have shown that harvesting of vertebrate species by many people living in Central and South American forests is frequently non-sustainable. Vasquez and Gentry (1989) also question the sustainability of fruit harvesting practices by rural people of Amazonian Peru because of excessive and destructive exploitation. The

potentially negative, indirect influences of harvesting on other animal species are rarely considered. Many animal and plant species harvested from tropical forests by humans are important in the diets of other animals; harvesting therefore may reduce or eliminate the availability of their food resources.

Palms are among the most frequently harvested plant species in the tropics (McCurrach 1960). Palms are harvested for food, building materials, cloth, ornaments, medicines and ritualistic purposes, and are of primary importance to many South American, Asian and African cultures (e.g., Moore 1973, Prance et al. 1987, Bates 1988, Davis 1988, Peters et al. 1989). Palms also figure prominently in the life cycles of a variety of insects and are important food sources to rodents, bats, ungulates and primates (see Uhl and Dransfield 1987 for review). Overexploitation is one of the major threats to the survival of many wild palm species (Uhl and Dransfield 1987). Although increased use of palms may provide economic benefits to rural people (Anderson 1988, Peters et al. 1989), some species, particularly high-potential market species, are being depleted by destructive harvesting (Vasquez and Gentry 1989).

Palms of the genus Phoenix are harvested throughout their range in tropical Africa and Asia. The fruit of Phoenix spp. have been important in Middle Eastern diets for

centuries and the leaves are widely used in Africa as a source of material for weaving (DeMason and Sekhar 1988, Uhl and Dransfield 1987). In this paper I outline the use of Phoenix reclinata Jacq. by the people of the Tana River in northeastern Kenya and by an endangered forest primate, the Tana River crested mangabey (Cercocebus galeritus galeritus). The Tana mangabey, endemic to a 60 km stretch of the lower Tana River, is a fruit and seed specialist that feeds heavily on P. reclinata (Homewood 1976). I examine the impact on the palm population of harvesting by people and palm fruit consumption by mangabeys. Specifically, I address questions concerning the nature of the harvesting, the preferential harvesting of different palm size classes, the role of mangabeys in seed dispersal and the potential effects of palm harvesting on fruit availability to the endangered primates.

Methods

Study Species

Phoenix reclinata is a dioecious, cluster palm with slender (<16 cm in diameter), often inclined trunks reaching over 10 m in height (McCurrach 1960). Leaves grow up to 2.5 m in length, are pinnate with proximal leaflets modified into spines, and show induplicate venation. Fruits are small (1.3-1.7 cm long by 0.9-1.3 cm wide) fleshy drupes, and vary in color from pale yellow to orange or dull red depending on ripeness. The mesocarp is 1-2 mm thick and is moist and

sweet when ripe. In the Tana River District of Northeastern Kenya, P. reclinata is abundant, and occurs primarily near river banks and in narrow belts separating riverine forests from woodlands and savannas.

Data Collection

Data on palm harvesting by people and fruit and seed consumption by mangabeys were collected between October 1987 and July 1989 in Mchelelo and Nkano forests. Phoenix reclinata is the most common plant species in the Mchelelo forest, occurring at a density of 194 individuals/ha and the second most common plant species in the Nkano forest, occurring at a density of 102/individuals ha (Chapter 2). Mchelelo is not used by local people but Nkano experiences a high degree of human exploitation.

I gathered information on palm use by people through personal observation and informal interviews with villagers living within and near the TRNPR. I divided palm uses into 6 broad categories developed by Prance et al. (1987): 1) food and beverage, 2) construction material, 3) technology, 4) remedy, 5) commerce and 6) other.

I collected data on palm harvesting in Nkano forest in April 1989, after the peak of palm harvesting by local people. I walked 2 kms of transects at 100 m intervals and recorded the following data: the number of palms or palm clusters within 3 m of each side of the transect, the size category of each palm or cluster, if the palm had been

harvested, and the level of harvesting. I used 4 size categories: 1) small, isolated individuals below 1 m in height, 2) bushy clusters up to 2 m in height that had not formed an obvious trunk, 3) palms with short trunks less than 2 m tall and 4) palms with trunks greater than or equal to 2 m in height. A palm was considered harvested if any parts had been cut or removed. Four levels of harvesting were defined based on the degree of cutting: 1) light (few leaves removed), 2) medium (up to half of all leaves removed), 3) heavy (often involving removal of all leaf fronds) and 4) topped (where the apical meristem of at least 1 trunk was removed).

Similar data, plus additional data on the sex of the palms, were collected for 1.1 km of transects in Mchelelo forest in June 1989. Sex was determined for reproductive plants by the presence of sexually distinct pendulous rachillae that bear the flowers and fruits; these rachillae generally wither and remain on the plant for extended periods after flowering and fruiting. Because the palms in Mchelelo are not exploited by the local people, Mchelelo was used as a control for comparison with data from Nkano. I used G-tests (Sokal and Rohlf 1980) to determine if the distributions of size classes were different for the 2 forests and if the frequency and level of harvesting among size classes deviated from uniform distributions.

I collected data on mangabey diets by scan sampling (Altmann 1974) during systematic monthly observations (approximately 1000 hrs.) of 2 groups of mangabeys, 1 each from the Mchelelo and Nkano forests (see Chapter 3). For each feeding record, I recorded the item eaten (e.g. leaf, flower, fruit, seed) and the stage of ripeness if the item was a fruit or seed. Seeds were recorded as the item eaten only when they were heard to crack. If a seed was swallowed with the rest of the fruit, or spit after sucking off the fleshy mesocarp, I recorded the item eaten as a fruit.

Results

Human use of P. reclinata along the Tana River is varied, and incorporates all of the 6 broad plant use categories (Table 4.1). All parts of the palm, including the roots, trunk, leaves and fruits, are utilized.

The distributions of size classes differ significantly between Mchelelo and Nkano ($G=276.8$, $df=3$, $p<0.001$) (Figure 4.1). Nkano has a higher than expected number of individuals in the small size class and a lower than expected number in the largest size class relative to Mchelelo ($p<0.001$).

There is significant heterogeneity in the distribution of harvested and unharvested palms by size class ($GI=104.4$, $df=3$, $p<0.001$); all but 1 cell deviates significantly from expected ($p<0.001$) with greater than expected numbers of palms harvested in the 2 largest size classes and fewer

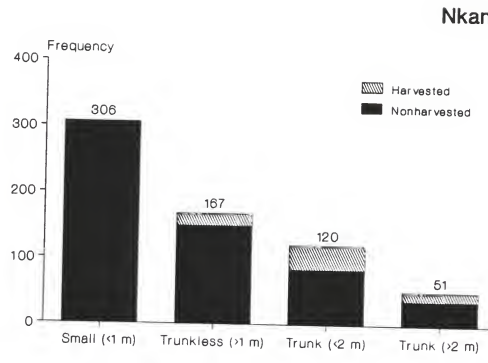
Table 4.1. Human uses of P. reclinata grouped into 6 broad categories. Plant parts utilized and harvesting methods employed are outlined.

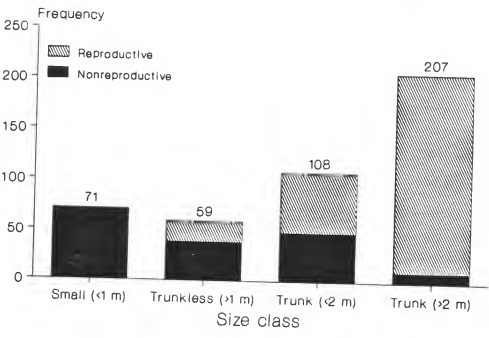
CATEGORY	PLANT PART/SPECIFIC USE	HARVESTING METHOD
Food and Beverage	a) palm heart infrequently used vegetable source	top palm, cut out palm heart, eat raw or boil.
	b) fruits infrequently used diet item	cut rachillae of unripe fruits, dip in water and hang until fruits ripen; eat raw or squeeze fruits in cloth and use extracted sweet mesocarp in baking.
	c) vascular bundles alcholic beverage	top palm, cover and hang gourd to one side to collect oozing, exudates, empty fermented contents from full gourds and cut a thin layer from top of trunk, replace cover and gourd and repeat daily until exudates stop flowing.
Construction	a) trunk poles for building construction	cut tall trunk at root base (used traditionally for constructing community or political buildings)
	b) leaf rachis wattle for constructing mud houses	cut frond at base, remove leaflets, mount horizontally between building poles before applying mud.
	c) leaflets building ties	strip leaflets from freshly cut leaf, use to bind poles, tie thatching to roofs, etc.
	d) leaf door entrances and covers	cut numerous, long fronds at base, sun dry, bind together in bundles, place over entrances.
Technology	a) leaf rachis fish traps	strip leaflets from freshly cut leaf, use flexible rachis and leaflets to construct oblong, funnel traps.
	b) leaf fans for stoking fires and fanning insects	cut unexpanded 'sword leaf', plait leaflets into wide, flat square fan with rachis as handle.
	c) leaflets strapping for hanging food and items that attract animals.	cut unexpanded 'sword leaf', sun dry, split and plait into wide, flat strapping, tie around rings of bananna leaves and suspend with strapping from ceiling.
	d) leaf rachis hand brooms	split rachis into numerous fibers, bundle together, fold in half and bind under fold with leaflets.

Table 4.1. -- Continued.

CATEGORY	PLANT PART/SPECIFIC USE	HARVESTING METHOD
Remedy	a) leaflets protecting healthy or curing diseased mango trees	cut leaflets, tie in a ring around lower trunk of mango tree, leave throughout flowering/ fruiting season.
Commerce	a) leaf sleeping and prayer mats baskets	cut unexpanded 'sword leaf', sun dry, split and plait strips for mats or weave into baskets.
	b) rachis floor mats	cut leaf, remove leaflets, split rachis linearly into thin strips, loosely bind strips into large mats.
Other	a) leaf ornamentation	cut leaf at base, bind, fold or weave as desired.
	b) roots insect larvae for fishing	dig through soil and leaf litter at root base to extract large wood grubs.
	c) leaf	fold in a variety of ways to make small dolls.

Figure 4.1. The number of harvested and unharvested palms in Nkano and the number of reproductive and nonreproductive palms in Mchelelo by size class.
a) harvested and unharvested palms by size class in Nkano; b) reproductive and nonreproductive palms in Mchelelo by size class.


Nkano
Frequency
400
300
200
100
0
306
167
120
51
Harvested
Nonharvested
Small (<1 m)
Trunkless (>1 m)
Trunk (<2 m)
Trunk (>2 m)

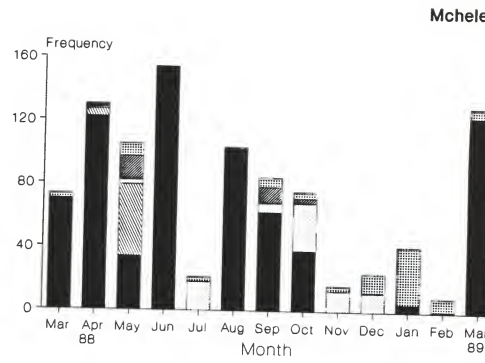

Mchelelo
Frequency
250
200
150
100
50
0
Reproductive
Nonreproductive
71
59
108
207
Small (<1 m)
Trunkless (>1 m)
Trunk (<2 m)
Trunk (>2 m)
Size class

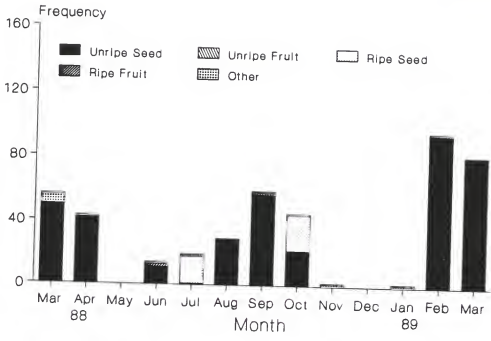
harvested in the smallest size class. Although there is no significant heterogeneity in the overall distribution of damage level by size class ($p>0.05$), there is significant within-cell heterogeneity due to a high frequency of topping in the largest size class ($GI=17.7$, $df=3$, $p<0.005$).

The majority of reproductive palms (84%) belonged to the 2 trunk-bearing size classes (Figure 4.1). Eighty percent (n=20) of the reproductive individuals counted in the smaller, trunkless size class were male. The proportion of male (60%) and female (40%) reproductive individuals was more equitable in the larger size class.

Phoenix reclinata accounts for up to 62% and 42% of the monthly diet of mangabeys in Mchelelo and Nkano, respectively. Phoenix reclinata accounts for 26% of the annual diet in Mchelelo and is eaten in some form during every month of the year. In Nkano, P. reclinata accounts for 18% of the annual diet and is eaten in some form during all but 1 month of the year. Ripe and unripe seeds account for the majority of the items taken in Mchelelo (84%) and Nkano (96%) and consumption of ripe fruits accounts for less than 3% in either forest (Figure 4.2), indicating mangabeys are major seed predators of P. reclinata. The 'other' category accounts for less than 10% of the total items consumed in either forest and includes thorns, open and unopened flowers, the pith of the leaf rachis, and seedlings.

Figure 4.2. The number of feeding observations on P. reclinata by month and item for mangabeys in the Mchelelo and Nkano forests.
a) Mchelelo; b) Nkano.


Mchelelo
Frequency
160
120
80
40
0
Mar
Apr
88
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Jan
Feb
Mar
89
Month


Nkano
Frequency
160
120
80
40
0
Unripe Seed
Unripe Fruit
Ripe Seed
Ripe Fruit
Other
Mar
Apr
88
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Jan
89
Feb
Mar
Month

Discussion

Phoenix reclinata is a very useful and important plant species for the people of the lower Tana River. Although direct economic benefits are limited to the sale of mats and baskets, the indirect benefits of free construction material and dietary supplements are numerous.

Although many of the human uses involve only the removal of leaves, several of the harvesting techniques are destructive. Cutting palm trunks for building, palm heart extraction, beer production, or for access to high growing leaves, damages the apical meristem and prevents further growth. Excessive leaf removal also may have a significant impact on reproduction and growth. Leaves are removed primarily from the 2 largest size classes. Data from Mchelelo indicate that fruit production by P. reclinata is rare until after a small trunk has begun to form. Preferential and excessive harvesting of the reproductive size classes may prevent or limit fruit production; no individuals were observed fruiting within 6 months after complete or near complete removal of leaves. This is also true for other palm species. Excessive harvesting of Sabal causiarum Cook leaves for hats in Puerto Rico also influences flowering and fruiting (Read 1988), and Woka palms (Livistona rotundifolia Lamark) of Indonesia frequently die as the result of excessive pruning (Davis 1988).

Preferential harvesting also may affect palm population structure. Differences in the distributions of size classes between Nkano and Mchelelo may be explained, in part, by the excessive harvesting of the larger size classes in Nkano. The lack of tall, trunked palms in Nkano is due to the extraction of this size class from the forest and possibly to growth suppression in other size classes due to frequent leaf pruning. The abundance of small, young plants in Nkano indicates that conditions for seedling establishment may be better in Nkano than Mchelelo and/or that undisturbed palms in Mchelelo tend to reproduce vegetatively. The more open understory and higher disturbance regime due to flooding in Nkano may enhance seedling establishment (Uhl and Dransfield 1987). There is no evidence, however, to suggest that the abundant young plants in Nkano will successfully reach the larger size classes; the majority of young plants occur in the center of the forest, an area where few large palms have established.

Throughout most of the year P. reclinata fruits and seeds are important food items for Tana mangabeys. Because P. reclinata is seasonal, producing fruit out of synchrony with other tree species (Chapter 2), mangabeys rely heavily on its fruits and seeds when few other fruits are available. The lower consumption of P. reclinata in Nkano relative to Mchelelo may be due to the lower abundance of reproductive individuals in Nkano, a higher abundance of alternative

fruit sources, or both. Species that fruit throughout the year, such as Ficus sycomorus, tend to dampen the effect of seasonal troughs in fruit availability and provide mangabeys with a more dependable resource base. In forests with a low abundance of figs or other species providing a continuous fruit resource, P. reclinata may be critical to the presence or persistence of mangabeys.

Mangabeys appear to play a much greater role in seed predation than seed dispersal. The occasional consumption however, of whole ripe seeds and the rejection of seeds after eating the sweet mesocarp of ripe fruits may aid P. reclinata seed dispersal and germination. Mangabeys frequently fill their cheek pouches with palm fruits before traveling to another food source and occasionally drop seeds as they move. Seeds extracted from the feces of mangabeys showed 100% germination success indicating that mangabeys can be effective seed dispersers.

Will human use of P. reclinata influence the long-term persistence of the palm, thereby having an impact on both people and endangered Tana mangabeys? It appears unlikely that present levels of human exploitation would result in the extirpation of this abundant palm; however, results indicate that such use may alter the population structure and influence reproduction. Although some of the human uses of P. reclinata may be sustainable at present levels, development of a local industry using palms (e.g., for mat

and basket production) could be devastating. Several of the human uses of the palms clearly are not sustainable. Individuals of P. reclinata with construction-size trunks have been removed from unprotected forests. Due to the lack of tall palms for the construction of ceremonial buildings, village leaders have set aside one small forest for pole production. Hyphaene compressa, another palm heavily utilized for thatching has been severely depleted from unprotected areas; people now travel more than 10 km to the reserve to harvest leaves (pers. obs.).

By eliminating palms or decreasing fruit production, palm harvesting degrades the habitat for the Tana mangabey and other frugivorous birds and mammals that rely heavily on the fruits and seeds of the palm. Given the continued elimination of forest area and increased fragmentation of forests due to agricultural expansion along the Tana River, activities further degrading the habitat will not be sustainable. Continued, but highly controlled, harvesting outside the reserve and cessation of harvesting within the reserve are necessary to provide benefits to both the humans and the endangered Tana River crested mangabey.

CHAPTER FIVE

TANA RIVER CRESTED MANGABEY HOME RANGE AND SPATIAL DEFENSE: EFFECTS OF FRUIT ABUNDANCE AND DISTRIBUTION

Introduction

Variability in primate ranging patterns have been related primarily to the availability and distribution of food resources (e.g., Altmann and Altmann 1970, Clutton-Brock 1977, Robinson 1986, van Schaik et al. 1983, Wrangham 1980). Species that depend on uniformly distributed, renewable resources tend to show an even use of space while, at the opposite extreme, species relying on highly patchy resources shift activities from one location to another as different patches become productive (Clutton-Brock and Harvey 1977, Struhsaker 1980, Struhsaker and Leland 1979, Terborgh 1983). Factors other than food also shape home range use. Such factors include weather (Chivers 1974, Marsh 1978b), location of traditional sleeping sites (Gittins and Raemaekers 1980, Rasmussen 1979), reproductive strategies of troop members (Rasmussen 1983) and intergroup interactions (Struhsaker 1975, Waser 1976, Isbell 1983, Srikosamatara 1986).

Although many primates maintain stable home ranges and patterns of intergroup relations throughout the year (Mitani and Rodman 1979), some studies have shown extreme variability in ranging and intergroup interactions for a species in different habitats and/or populations (e.g., Cercopithecus aethiops, Chapman and Fedigan 1984, Kavanagh 1981; Cercopithecus mitis, Butynski 1990; Colobus badius Marsh 1981b, Struhsaker and Leland 1979; Colobus guereza, Oates 1977; Macaca sylvanus, Mehlman 1989; Papio ursinus, Hamilton et al. 1976; Presbytis entellus, Yoshiba 1968; Presbytis melalophos, Bennett 1986). These studies document differing strategies between groups or populations of a species. Few data exist, however, on variability of defense of space within groups of a single population.

Homewood (1976) and Waser and Homewood (1979) noted for the Tana River crested mangabey (Cercocebus galeritus galeritus) that any generalizations about defense were precluded by the high intragroup variability in defense. The extent of variation in mangabey intergroup behaviors is striking, ranging from descriptions of intergroup fighting to peaceful, non-aggressive encounters in which groups sometimes merge. The Tana mangabey, therefore, is an ideal subject for investigating factors influencing use and defense of space.

In this chapter, I quantify and examine variation in use and defense of space by the Tana River crested mangabey.

Specifically, I address the question of how the availability and distribution of food resources influence ranging patterns and spatial defense, and how intergroup interactions, in turn, influence ranging patterns.

Methods

Data Collection

I studied 2 groups of mangabeys in Mchelelo forest and 1 group in Nkano forest. Group sizes averaged 18 (range 14-18) and 28 (range 24-29) for the North and South Mchelelo groups, respectively, and 16 (range 14-17) for the Nkano group. Age-sex composition was similar for the 3 groups (see Chapter 6).

A grid of trails was cut at approximately 50 and 100 m intervals in both forests. Plastic flagging or marked aluminum strips were placed every 50 m along trails or along compass bearings where no trails were cut. The study areas were mapped and overlaid with a grid representing 0.25 ha (50m x 50m) quadrats. I chose a relatively small quadrat size (see Waser and Floody 1974) because of the small size of the study forests (17 and 38 ha for Mchelelo and Nkano, respectively). A 0.25 ha quadrat allowed me to compare the group's use of space to the distributions of selected tree species, which were analyzed at this scale.

I collected data on mangabey movements and use of space for 3 days each month from January 1988-March 1989 for each Mchelelo group, and March 1988-March 1989 for the Nkano

group (Chapter 3). I followed groups from 0700-1830 hrs each day; every half hour, following a behavioral scan (Chapter 3), I plotted the location of all individuals that could be found in a 5-minute period. I noted all quadrats that were occupied by at least 1 individual and determined the quadrat location of the group's center-of-mass (see Altmann and Altmann 1970, Waser and Floody 1974). I assumed the distance moved by the group in each half-hour period equalled the straight line distance between consecutive locations of the center-of-mass. The sum of all half-hour "step distances" was used as an estimate of total daily distance moved. I also calculated the turning angle between each pair of 1/2 hr steps (not calculated or included in summary statistics if group did not move) and counted the number of times a group crossed its own path.

I recorded the time and location of all adult male mangabey long-calls (defined as loud-call or long-range vocalization by Homewood 1976 and Waser 1982) on daily range maps. The group which initiated a long call was determined when possible and response to the long calls by the study group was recorded.

Time, duration, and outcome of all inter-group interactions were recorded ad libitum. I also noted age, sex, and behavior of interactants and plotted the location of all interactions on daily range maps.

I collected ranging data simultaneously on North and South Mchelelo groups on 25 days with the help of field assistants. Simultaneous group follows were distributed throughout the study period and conducted only when the South group was present in the Mchelelo forest (see Chapter 3). From daily range maps for both groups, I calculated distance between neighboring groups each half-hour, number of half-hour periods when groups were less than 100 m apart, and number of half-hour periods when groups occupied the same 0.25 ha quadrat. Simultaneous follows allowed me to measure the effects of neighboring groups on movements and use of space, and to accurately assess the response of groups to long-calls of neighboring males.

Data Analysis

To examine variability in mangabey behavior throughout a group's home range, I tested for differences in the proportion of time spent in 4 behaviors while located in high-use quadrats (those accounting for a cumulative 50% of all sightings) and low-use quadrats. The proportion of time spent eating, foraging, moving, and engaged in other activities while the group's center-of-mass was located in a given quadrat was estimated by calculating the mean percent time spent in each activity during each behavioral scan (see Chapter 3). Mean percent diet species and diet item consumption was calculated similarly.

I classified the distribution of selected plant diet species as patchy or uniform to test the effect of plant abundance and distribution on mangabey ranging patterns and intergroup behaviors. I used only those plant diet species that accounted for more than 2.5% of the estimated annual diet of both the North and South Mchelelo groups (N=9, Appendix A). I defined a patchy species as having fewer than 2 individuals/ha or a Morisita's index of dispersion greater than 2.0. Species that were highly abundant in the forest (>15 individuals/ha), had Morisita's indices less than 2.0, or tended to occur in larger, continuous clusters ($\geq$ 0.25 ha) were defined as uniform. This classification scheme resulted in one ambiguous species (Oncoba spinosa with 6.49 individuals/ha and $I_{\S}$=2.67) that was dropped from the analysis.

I used 3 categories to describe monthly intergroup behaviors according to the extent and outcome of intergroup interactions: avoid, fight, and merge. Avoid months were defined as those months in which no intergroup interactions were recorded and the South group was resident in Mchelelo forest less than 50% of the days monitored. Fight months were defined as months in which at least one fight was recorded between groups. Merge months were defined as those months in which no fights occurred when both groups simultaneously occupied the same 0.25 ha quadrat or residency of South Mchelelo group was greater than 50%.

I used both parametric and nonparametric statistical methods for data analyses. Spearman's Rank correlations were used to examine associations between daily and monthly travel patterns and the proportion of time spent in various activities (e.g., eating, foraging and moving), the type of dietary items consumed (e.g., fruit versus invertebrate), and measures of fruit availability (Chapter 2). I also used Spearman's Rank correlations to examine associations between patterns of travel and the frequency of long-calls. Student's t-tests were used to test for differences in the means of tree density, tree species diversity, and percent time spent in various behaviors between high-use and low-use quadrats.

I used analysis-of-variance techniques (ANOVA) to evaluate the effects of independent variables (month, season, group membership, neighboring group presence, and intergroup behaviors) on mangabey use of space, patterns of travel, and frequency of long-calls. Arcsin square-root and square-root transformations were used on proportional and count data, respectively, to meet the assumptions of equal variances (Sokal and Rohlf 1981). I tested for significance with F-tests using partial sums of squares (Type III), which adjust each effect for all other effects in the model and are unrelated to cell frequencies (Freund and Littell 1981). Multiple means comparisons of the distribution of foods eaten (uniform versus patchy) and the frequency of long-

calls given as a function of intergroup behavior (avoid, fight, and merge) were made when ANOVA indicated significant differences. All analyses were performed on the SAS statistical package (SAS 1985).

Results

Use of Space

Mangabeys from the North Mchelelo, South Mchelelo and Nkano groups were sighted in a total of 75, 72, and 80 quadrats, respectively (Figures 5.1-5.3). This represents home range areas of 19 and 20 ha for the North Mchelelo and Nkano groups, and a range area of 18 ha for the South Mchelelo group only when in the Mchelelo forest. A "taut-string line" (Waser and Floody 1974), enclosing all ad libitum South Mchelelo group sightings outside the Mchelelo forest, increased the home range estimate for this group to 70 ha (Figure 5.4).

Use of space by each group was not distributed evenly. The number of observations spent in a quadrat plotted against the rank of that quadrat showed that North Mchelelo group mangabeys spent over 50% of their time in 14 quadrats, which corresponds to 3.5 ha, or 19% of their total home range (Figure 5.1). The South Mchelelo and Nkano groups spent over 50% of their time in 16 quadrats. This corresponds to 4 ha, or 22% of the South group's total range in the Mchelelo forest (Figure 5.2), and 4 ha, or 20% of the total home range of the Nkano group (Figure 5.3).

Figure 5.1. Cumulative frequency of sightings of one or more North Mchelelo group mangabeys versus rank order of 0.25 ha quadrats. Quadrats were ranked with respect to the number of sightings occurring in each. The areas accounting for 50 and 100% of all sightings are designated.

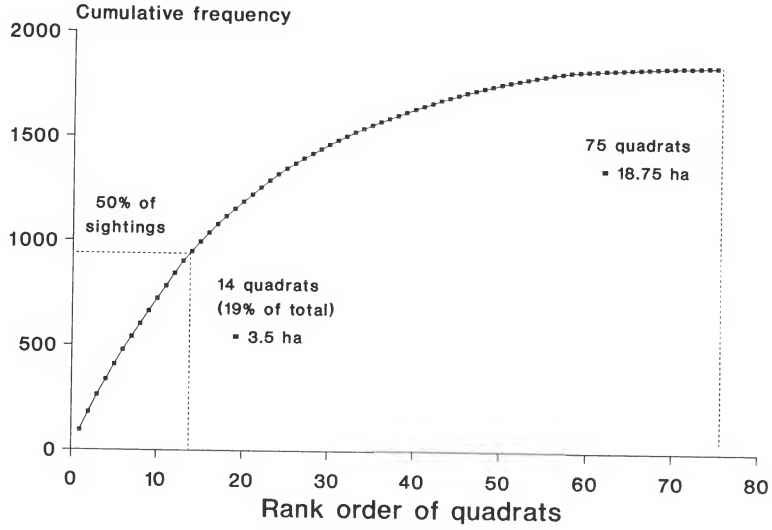

Cumulative frequency
2000
1500
1000
500
0
50% of
sightings
14 quadrats
(19% of total)
▪ 3.5 ha
75 quadrats
▪ 18.75 ha
0
10
20
30
40
50
60
70
80
Rank order of quadrats

Figure 5.2. Cumulative frequency of sightings of one or more South Mchelelo group mangabeys versus rank order of 0.25 h quadrats. Quadrats were ranked with respect to the number of sightings occurring in each. The areas accounting for 50 and 100% of all sightings are designated.

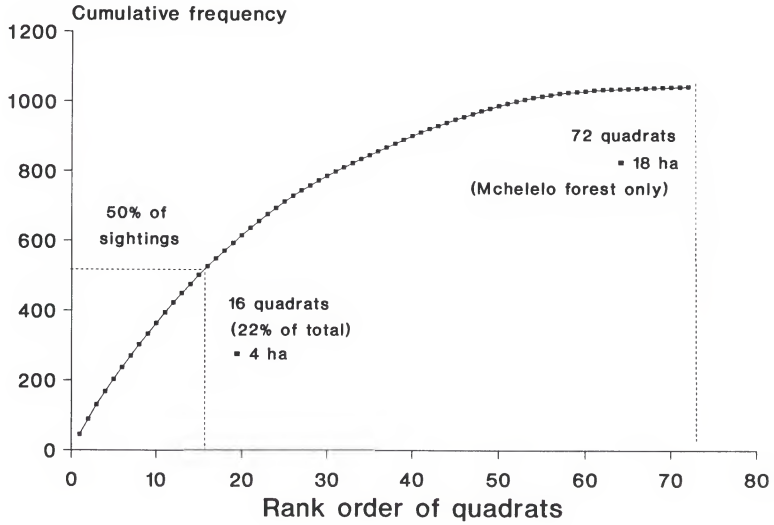

Cumulative frequency
1200
1000
800
600
400
200
0
0
10
20
30
40
50
60
70
80
Rank order of quadrats
72 quadrats
▪ 18 ha
(Mchelelo forest only)
50% of
sightings
16 quadrats
(22% of total)
▪ 4 ha

Figure 5.3. Cumulative frequency of sightings of one or more Nkano group mangabeys versus rank order of 0.25 ha quadrats. Quadrats were ranked with respect to the number of sightings occurring in each. The areas accounting for 50 and 100% of all sightings are designated.

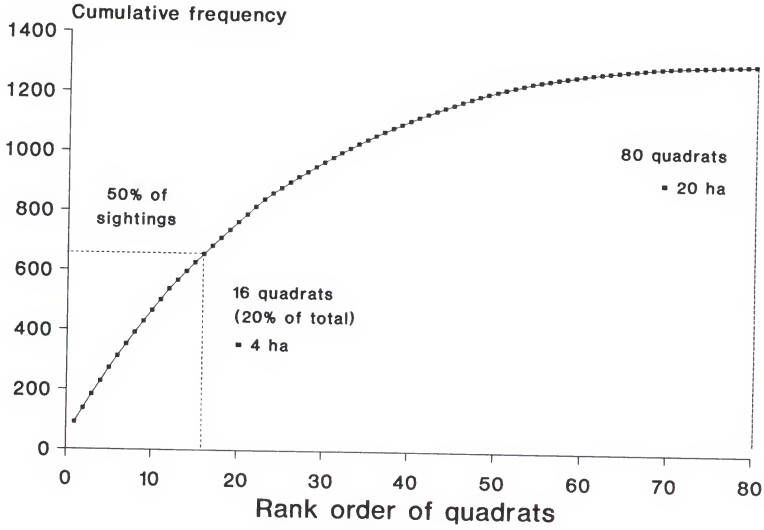
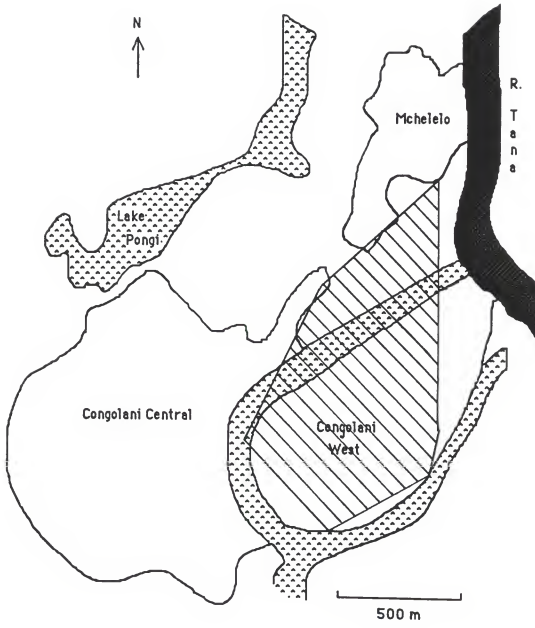

Cumulative frequency
1400
1200
1000
800
600
400
200
0
50% of
sightings
16 quadrats
(20% of total)
▪ 4 ha
80 quadrats
▪ 20 ha
0
10
20
30
40
50
60
70
80
Rank order of quadrats

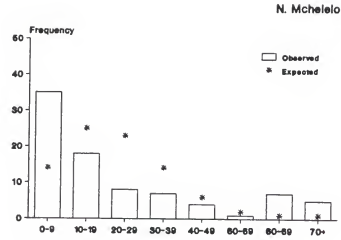
Figure 5.4. Taut-string line (shaded with diagonal lines) enclosing all ad libitum sightings of South Mchelelo group when the group ranged outside the Mchelelo forest.

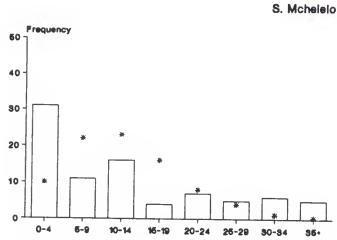

N
R.
T
e
n
e
Michelelo
Lake
Pongi
Congolani Central
Congolani
West
500 m

I tested the distribution of sightings throughout each group's range against a Poisson distribution to determine if their use of space was random. I found significant deviations in the distribution of sightings from the expected Poisson distributions for all 3 groups (N. Mchelelo: $X^2=29.8$, df=6, $P<0.0001$; S. Mchelelo: $X^2=31.4$, df=6, $p<0.0001$; Nkano: $X^2=55.6$, df=7, $p<0.0001$). As indicated above, some quadrats were used much more than expected, some less than expected (Figure 5.5). This uneven pattern of use is evident also from the percent of total sightings recorded within each quadrat for the 3 study groups (Figures 5.6 and 5.7). Few quadrats were used intensely (accounting for >4% of the total observations), many were used less frequently.

Attributes of high-use quadrats. I tested for differences in mangabey behaviors in high-use quadrats (quadrats accounting for a cumulative 50% of total sightings and individually $\geq$ 2% of total sightings) and low-use quadrats to determine if mangabeys frequented certain quadrats to feed (eat and forage) or simply moved through them to reach other locations. There were no significant differences in the amount of time spent eating, foraging or moving in high- versus low-use quadrats for any of the study groups (One-way Student's t-tests, $p>0.05$). The variance in behaviors, however, was significantly less in high- versus low-use quadrats for each study group (F-ratio for equal

Figure 5.5. Frequency distributions of intensity of quadrat use. Asterisks indicate the values expected if quadrat occupancy were random (following a Poisson distribution).
a) Frequency distribution for N. Mchelelo group; b) Frequency distribution for S. Mchelelo group; c) Frequency distribution for Nkano group.


N. Mchelelo
Frequency
60
40
30
20
10
0
Observed
Expected
0-9
10-19
20-29
30-39
40-49
50-59
60-69
70+


S. Mchelelo
Frequency
60
40
30
20
10
0
0-4
5-9
10-14
15-19
20-24
25-29
30-34
35+

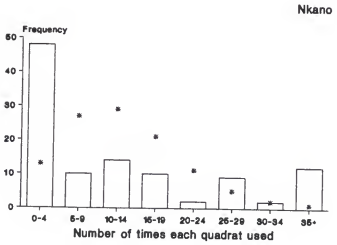

Nkano
Frequency
60
40
30
20
10
0
0-4
5-9
10-14
15-19
20-24
25-29
30-34
35+
Number of times each quadrat used

Figure 5.6. Occupancy of each 0.25 ha quadrat by North and South Mchelelo groups; percent occupancy is divided into 1 of 5 intensities of use.

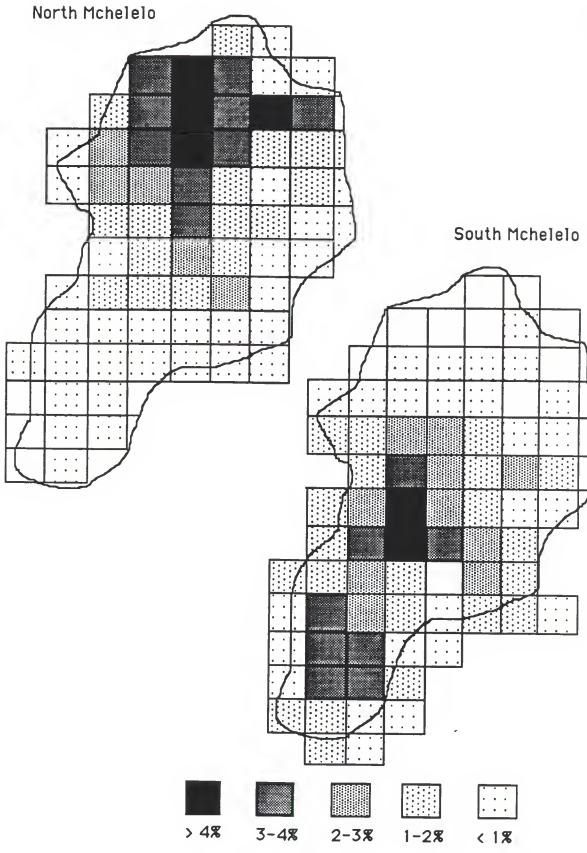
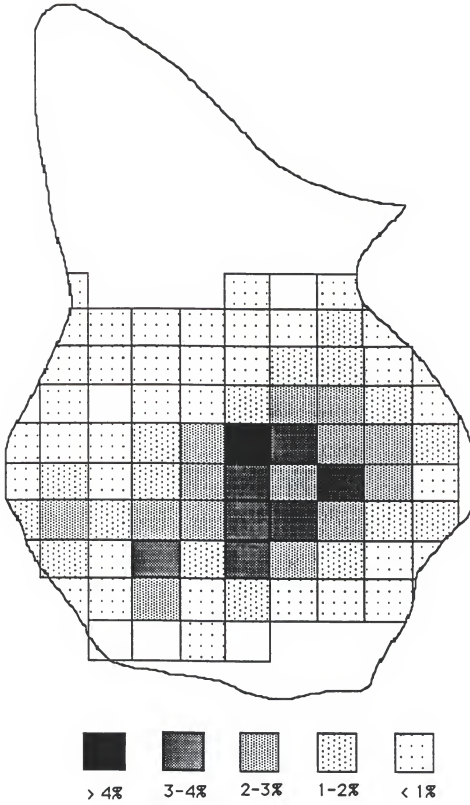

North Mchelelo
South Mchelelo
> 4%
3-4%
2-3%
1-2%
< 1%

Figure 5.7. Occupancy of each 0.25 ha quadrat by Nkano group; percent occupancy is divided into 1 of 5 intensities of use.


> 4%
3-4%
2-3%
1-2%
< 1%

variances >2.5, df 59,13, $p<0.05$), indicating that mangabey behavior was more consistent in high-use quadrats.

I also tested for differences in mean species diversity and mean densities of the 10 top mangabey diet plant species (Appendix B) in high- and low-use quadrats to determine if high-use quadrats differed vegetatively from low-use quadrats. There were no significant differences in mean species diversity between high- and low-use quadrats for North Mchelelo, South Mchelelo, or Nkano (Student's two-sample t-test, $p>0.05$). Differences in diet species densities were significantly higher in high-use quadrats of the North Mchelelo group for Phoenix reclinata ($t=2.1$, $df=63$, $p=0.04$) and Oncoba spinosa ($t=2.8$, $df=63$, $p=0.01$). High-use quadrats of the South Mchelelo group had significantly higher densities of Alangium salviifolium ($t=2.0$, $df=63$, $p=0.04$) and Ficus sycomorus ($t=2.6$, $df=63$, $p=0.02$), and those of the Nkano group had significantly higher densities of Pachystela msolo ($t=3.9$, $df=52$, $p=0.0004$) and Alangium salviifolium ($t=2.9$, $df=52$, $p=0.006$).

Diet species densities in high- versus low-use quadrats, however, generally did not correspond with differences in the consumption of these species by mangabeys. There were no significant differences in the proportion of different diet species eaten in high- and low-use quadrats for the North Mchelelo group (Student's two sample t-test, $p>0.05$). The South Mchelelo group ate a significantly higher proportion

of Saba comorensis in high- versus low-use quadrats (t=2.6, df=64, p=0.02), and the Nkano group ate significantly higher proportions of Pachystela msolo (t=3.0, df=76, p=0.004) and Aporrhiza paniculata in high- versus low-use quadrats (t=3.5, df=76, p=0.002).

In general, there appear to be no particular attributes that characterize high- and low-use quadrats. Use of space by mangabeys may be influenced more by the seasonal availability of food resources.

Seasonal variation. The diversity of quadrats used by mangabey groups (Shannon-Wiener Index of diversity, H') varied between months; in some months mangabeys spent a disproportionate amount of time in few quadrats (Table 5.1). If mangabeys track seasonally available fruit resources, then their use of space at any given time should correlate with the spatial distribution of fruits being eaten at that time (Robinson 1986). I examined associations between frequency of quadrat use by each mangabey group and the frequency of occurrence in a given quadrat of the top 5 diet species of each month (Table 3.5). I used only those months for which data on frequencies of all trees in the top 5 diet species were available, and I excluded Phoenix reclinata from the North and South Mchelelo group analyses because of the overwhelming abundance of the palm throughout the forest. There were significant correlations for 8 of 11 months, 3 of 9 months, and 7 of 12 months (for which data

Table 5.1. Mean diversity of quadrat use (H'), mean number of unique quadrats entered, mean distances travelled, mean half-hour step distances, mean turning angles, and mean number of path crossings by month for the 3 study groups.

a) North Mchelelo

Month	H'	Quad Entries	Distance Travelled (m)	1/2 Hr Steps (m)	Turning Angles	Path Cross
Feb 88	3.3	35	1237	52	64	7
Mar	3.4	41	1321	55	58	4
Apr	3.7	51	1307	55	71	2
May	3.2	34	1266	53	45	4
Jun	3.6	50	1053	44	52	1
Jul	3.6	44	1282	54	54	3
Aug	3.3	35	939	39	58	2
Sep	3.6	43	1069	46	53	3
Oct	3.4	40	1390	60	55	3
Nov	3.1	27	1129	49	56	4
Dec	3.4	38	1133	50	50	3
Jan 89	3.5	41	1076	47	48	2
Feb	3.1	29	980	44	50	5
Mar	3.4	44	756	34	50	1

b) South Mchelelo

Feb 88	3.6	43	1368	56	61	7
Mar	3.6	47	1158	46	56	3
Apr	3.1	28	1328	59	55	4
Jun	3.6	49	1042	44	60	2
Jul	3.3	34	1089	47	73	2
Sep	3.4	40	1351	60	55	4
Oct	3.7	45	1589	75	79	3
Nov	3.5	41	1207	51	62	2
Dec	3.0	24	1397	61	45	10
Jan 89	3.6	45	1194	53	52	4

c) Nkano

Mar 88	3.4	34	1112	47	70	2
Apr	3.5	46	1592	67	64	3
Jun	3.4	42	1142	49	65	3
Jul	3.7	51	1268	54	55	2
Aug	2.8	19	955	42	82	2
Sep	3.4	41	1299	56	65	4
Oct	3.6	44	1617	70	70	5
Nov	2.8	23	887	39	72	5
Dec	3.1	31	1060	47	87	6
Jan 89	3.1	31	1040	46	72	4
Feb	3.1	33	740	33	70	3
Mar	3.3	39	860	40	55	0

were available) for the North Mchelelo, South Mchelelo, and Nkano groups, respectively (Table 5.2). The months for which correlations were not significant, however, were months in which grasses occurred in the top 5 diet species and/or in which invertebrate consumption was high (Tables 3.5 and 3.6).

Movements

Daily path length and patterns of movement. Mean daily path length was 1138 m (range=588-1728 m, n=42 days), 1278 m (range=779-1744 m, n=24 days), and 1141 m (range=646-2039 m, n=34 days) for the North Mchelelo, South Mchelelo, and Nkano groups, respectively. Rate of movement, or group speed, measured as the mean half-hour step distance, was 48 m (range=0-199 m) for North Mchelelo, 52 m (range=0-221 m) for South Mchelelo, and 49 m (range=0-260 m) for Nkano group. The distribution of distances moved in half hour periods deviated significantly from expected Poisson distributions for all 3 groups (X^2=19.2, df=8, P<0.01; X^2=28.1, df=8, p<0.0004; X^2=87.9, df=8, p<0.0001 for N. Mchelelo, S. Mchelelo, and Nkano, respectively). There were more short and more long movements than would be expected if group speeds were random (Figure 5.8), indicating that groups moved rapidly through some areas and spent more time in others.

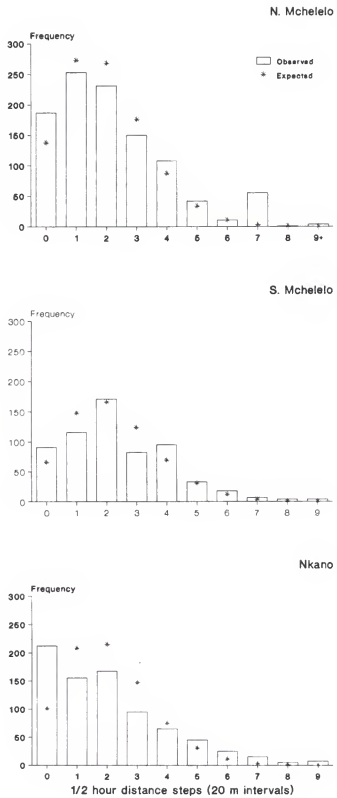
Half-hour turning angles indicated that all groups tended to move ahead ($\leq 90^0$ from the direction moved the

Table 5.2. Spearman's Rank correlation coefficients (r_{xy}) between frequency of quadrat use by mangabeys and frequency of occurrence of top 5 plant diet species each month for the North Mchelelo, South Mchelelo, and Nkano groups. (-) indicates that ranging data or plant frequency data were not available for all top 5 diet species that month.

Month	North Mchelelo r_{xy}	South Mchelelo r_{xy}	Nkano r_{xy}
Feb 88	0.38**	-0.01	-
Mar	-0.05	0.19	0.12
Apr	0.29**	0.35**	-0.10
May	0.23*	-	-
Jun	0.55**	0.05	0.01
Jul	0.35**	0.44**	0.19
Aug	-	-	0.08
Sep	-	-0.03	0.28**
Oct	0.22*	-	0.37**
Nov	-0.02	-0.08	0.28**
Dec	0.59**	-0.04	0.28**
Jan 89	0.25**	0.43**	0.50**
Feb	0.10	-	0.45**
Mar	-	-	0.50**

** $p<0.05$, $n=58$
* $p<0.1$, $n=58$

Figure 5.8. Frequency distributions of half-hour distance steps in intervals of 20 m. Asterisks indicate values expected if distance steps were distributed randomly (following a Poisson distribution).
a) Frequency distribution for N. Mchelelo group; b) Frequency distribution for S. Mchelelo group; c) Frequency distribution for Nkano group.

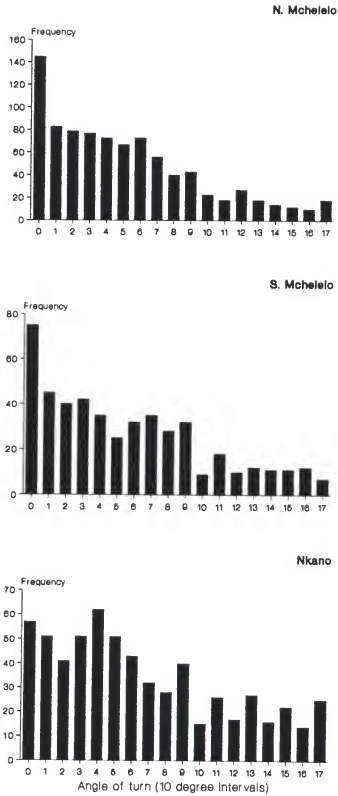

N. Mchelelo
Frequency
300
250
200
150
100
50
0
Observed
Expected
0 1 2 3 4 5 6 7 8 9+
S. Mchelelo
Frequency
300
250
200
150
100
50
0
0 1 2 3 4 5 6 7 8 9
Nkano
Frequency
300
250
200
150
100
50
0
0 1 2 3 4 5 6 7 8 9
1/2 hour distance steps (20 m intervals)

previous half hour) more than backtrack ($>90^0$) (Figure 5.9). Turning angles, however, were not always good indices of backtracking. A series of small turning angles, all in the same direction, often indicated forward movement but resulted in backtracking. The number of times a group crossed its own path therefore, may be a better index of backtracking. Number of daily path crossings varied from 0-13 ($\bar{x}$=3.4) for the North Mchelelo group, 0-10 ($\bar{x}$=3.6) for the South Mchelelo group, and 0-9 ($\bar{x}$=3.4) for the Nkano group. Although number of daily path crossings was significantly related to mean turning angle, turning angle was a weak predictor of path crossings, accounting for only 17% of the variance.

Despite differences in group size and habitat, there were few significant effects of group membership on daily distance travelled and measures of travel pattern. Group membership had a significant effect only on turning angle ($F=8.51$, $df=2,11$, $p<0.002$); least square means comparisons showed the Nkano group had higher average turning angles than either of the Mchelelo groups.

Seasonal variation. There was considerable monthly variation in the average daily distance travelled, mean rate of group movement, mean turning angles, and mean path crossing for all 3 groups (Table 5.1). I examined associations between mean daily path length and travel

Figure 5.9. Frequency distributions of half-hour turning angles in 10 degree intervals. a) Frequency distribution for N. Mchelelo group; b) Frequency distribution for S. Mchelelo group; c) Frequency distribution for Nkano group.


N. Mchelelo
Frequency
160
140
120
100
80
60
40
20
0
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17
S. Mchelelo
Frequency
80
60
40
20
0
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17
Nkano
Frequency
70
60
50
40
30
20
10
0
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17
Angle of turn (10 degree intervals)

patterns and monthly measures of food availability (Chapter 2) to determine if mangabeys adjusted movements to take advantage of resource availability. If movements depend on encounter rates with food (see Robinson 1986), then mangabeys should travel further and show less tendency to backtrack during months when resources are scarce. The results were equivocal; mean path length was significantly correlated with ripe fruit availability for the South Mchelelo group only ($r=-0.66$, $n=10$, $p<0.04$).

Alternatively, monthly movements may be influenced by the spatial distribution and renewability of food items used each month. Because foods of plant origin, especially ripe fruit, often are less homogeneously distributed and/or have slower renewal rates than invertebrates (Robinson 1986, Waser and Wiley 1980), mangabeys should backtrack less, have longer daily path lengths and longer half-hour step distances when feeding on ripe fruit trees. This association was not apparent for any of the 3 groups; there were no significant correlations between mean monthly path length or tendency to backtrack and the proportion of ripe fruits or invertebrates in the diet (Spearman's Rank correlations, $p>0.05$).

Intergroup Behavior

Group range overlap. The home range of South Mchelelo group overlapped almost completely with that of North Mchelelo (Figure 5.6). Overlap of South Mchelelo group's

home range by North Mchelelo group was less extensive (approximately 25%) because the North group never left Mchelelo forest. The amount of overlap between the 2 groups varied considerably by month, with the South Mchelelo group generally spending a larger proportion of time in the overlap zone than the North Mchelelo group (Figure 5.10). The Nkano group also overlapped with an unhabituated mangabey group that ranged primarily in the northern section of the Nkano forest and possibly a third group that occasionally visited from the nearby Mnazini forest.

I tested for differences in quadrat use, travel patterns and distances traveled by the North Mchelelo group when South Mchelelo group was present and absent from Mchelelo forest to determine if the presence of a neighboring group influenced North group's movements and/or use of space. After controlling for the effects of month, the presence of South group appeared not to influence distance traveled, but did influence travel patterns and use of space (ANOVA, Table 5.3). Least square means showed that the amount of backtracking, as measured by mean turning angle ($p=0.007$) and number of path crossings ($p=0.04$), was significantly higher when South group was present. North group also restricted its use of space when South group was present; the diversity of quadrats used and the number of unique quadrats entered by North group were significantly lower when South group was present.

Figure 5.10. Degree of monthly overlap by North Mchelelo group (solid line) and South Mchelelo group (broken line) and the area of overlap in hectares (bars).

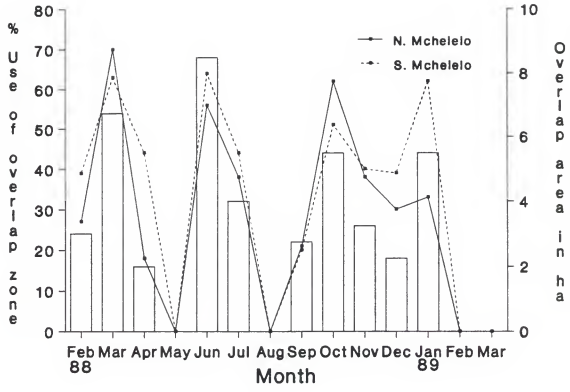

% Use of overlap zone
Overlap area in ha
N. Mchelelo
S. Mchelelo
80
70
60
50
40
30
20
10
0
10
8
6
4
2
0
Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec Jan Feb Mar
88
89
Month

Table 5.3. ANOVA results for effect of South Mchelelo group presence and month on distance traveled and measures of travel pattern and use of space by North Mchelelo group. F-statistics are calculated from Type III partial sums of squares.

Source	df	Sum of Squares	Mean Squares	F	P>F
Distance					
Month	13	996995.2	76691.9	3.39	0.001
Presence	1	1.0	1.0	0.00	0.994
Error	42	949264.3	22601.5		
Turning Angle					
Month	13	2701.5	207.8	2.01	0.043
Presence	1	832.3	832.3	8.07	0.007
Error	42	4333.0	103.2		
Path Crossing					
Month	13	11.3	0.9	1.96	0.05
Presence	1	1.9	1.9	4.25	0.04
Error	42	18.6	0.4		
Quad Entries					
Month	13	271.1	20.9	1.48	0.167
Presence	1	84.7	84.7	6.00	0.019
Error	42	592.8	14.1		
Quad Diversity					
Month	13	0.7	0.1	1.31	0.247
Presence	1	0.2	0.2	4.93	0.032
Error	42	1.7	0.1		

Frequency of male long calls. The numbers of long calls given by adult males of North and South Mchelelo groups were relatively consistent among months and seasons (Table 5.4); ANOVA showed no significant effect of month or season on calling by North or South Mchelelo males, or both groups combined ($p>0.05$). South group's presence in the Mchelelo forest also had no effect on the frequency of calling by North group males (ANOVA, $p>0.05$). Month but not season had significant effects on numbers of long calls given by Nkano group males ($F=4.1$, $df=11,22$, $p<0.002$), males of the neighboring, unhabituated group ($F=8.64$, $df=11,22$, $p<0.0001$), unidentified callers ($F=3.73$, $df=11,22$, $p<0.004$), and all calls combined ($F=5.3$, $df=11,22$, $p<0.0004$). The effect of month on calling, however, was due to extensive counter-calling between several males during November, a month of an attempted group takeover. When November was eliminated from the analysis the differences are no longer significant.

There were no significant correlations between long-calls and monthly total fruit availability, unripe fruit availability, or the percent of ripe and unripe fruit in the diet for all 3 study groups (Spearman's Rank correlation, $p>0.05$). Ripe fruit availability was significantly correlated only with the number of long-calls given by North group males ($r=0.83$, $p<0.0001$, $n=14$).

Table 5.4. Number of adult male long-calls by study group and month. North refers to long-calls given by the North Mchelelo group males. South M refers to long-calls given by the South Mchelelo group males while present in Mchelelo forest and South C refers to long-calls given by the South Mchelelo group males while in the neighboring Congolani forest. Alien refers to long-calls given by males of a second, unhabituated group in Nkano forest, and Unk represents long-calls of unidentified males in the Nkano forest.

a) North and South Mchelelo

Month	North	South M	South C	Total	N (days)
Feb 88	17	9	1	28	5
Mar	19	19	0	42	6
Apr	18	28	13	61	6
May	16	18	0	34	3
Jun	14	20	8	43	5
Jul	9	37	14	62	6
Aug	13	4	0	17	3
Sep	15	37	1	54	5
Oct	22	14	0	38	4
Nov	34	31	1	69	6
Dec	17	9	0	26	4
Jan 89	24	25	0	49	5
Feb	8	2	0	10	3
Mar	9	5	0	14	3

b) Nkano

Month	Nkano	Alien	Unk	Total	N (days)
Mar 88	6	0	49	55	3
Apr	36	25	3	64	3
Jun	43	27	3	73	3
Jul	24	15	7	46	3
Aug	5	9	7	21	1
Sep	20	28	20	68	3
Oct	20	22	1	43	3
Nov	37	85	15	137	3
Dec	32	28	5	65	3
Jan 89	37	30	7	74	3
Feb	30	36	5	71	3
Mar	19	16	5	40	3

Variability in intergroup interactions. Fourteen months of observations from Mchelelo forest were classified by intergroup interactions; May and August 1989 were excluded because of severe flooding and small sample size, respectively. Seven of 14 months were classified as fight months, 4 as merge months, and 3 as avoid months (Table 5.5).

Avoid months were characterized by limited, non-overlapping ranging patterns; the North group remained mostly in the north sector of the forest and the South group remained in the south sector (Figure 5.11). Although long calls were frequent, immediate vocal response (within 2 min. of the initial call) by neighboring group males was rare and groups tended to move away from the direction of the call.

Merge months were characterized by more overlap in ranging patterns; both groups frequently crossed the other's travel path and often traveled in parallel progressions (Figure 5.12). Immediate vocal responses to long calls were more frequent than during avoid months and calls often resulted in approaches by the neighboring group. When groups merged, they formed close, non-aggressive associations moving together for periods of up to several hours. During these associations, each group remained largely discrete but occasionally individuals of the 2 groups intermingled, foraging side-by-side, grooming, and sexually presenting to members of the neighboring group. Intragroup herding by

Table 5.5. Intergroup behavior categories and measures of proximity and fighting by month. F, M, and A designate fight, merge, and avoid months, respectively. N includes all 12-hr observation days and days for which only presence or absence of South group was determined.

Month	Intergroup Behavior Category	% S. Group Residency	% Scans Groups Merged	% Scans Groups <100m Apart	% Encounters Resulting in Fights	N (days)
Jan 88	F	62	10	-	40	13
Feb	F	50	7	15	40	7
Mar	F	94	40	53	56	9
Apr	F	35	0	1	100	13
Jun	M	55	0	14	0	9
Jul	M	43	4	28	0	7
Sep	M	54	7	13	0	11
Oct	M	50	6	21	0	7
Nov	F	93	7	18	22	7
Dec	A	18	0	11	0	10
Jan 89	F	52	5	4	100	13
Feb	A	0	0	0	0	8
Mar	A	19	0	0	0	13
Apr	F	14	4	4	100	9

Figure 5.11. Daily travel paths by North and South Mchelelo groups during one day of a month of intergroup avoidance. Timing and location of adult male long-calls are plotted for North (ovals) and South (rectangles) groups.

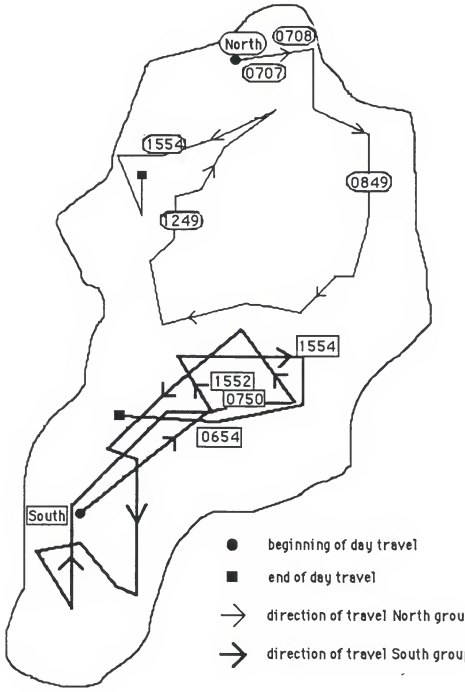
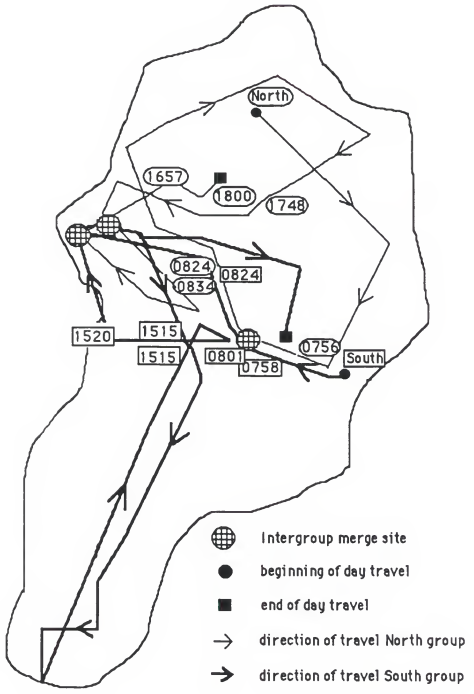

North
0708
0707
1554
0849
1249
1554
1552
0750
0654
South
beginning of day travel
end of day travel
direction of travel North group
direction of travel South group

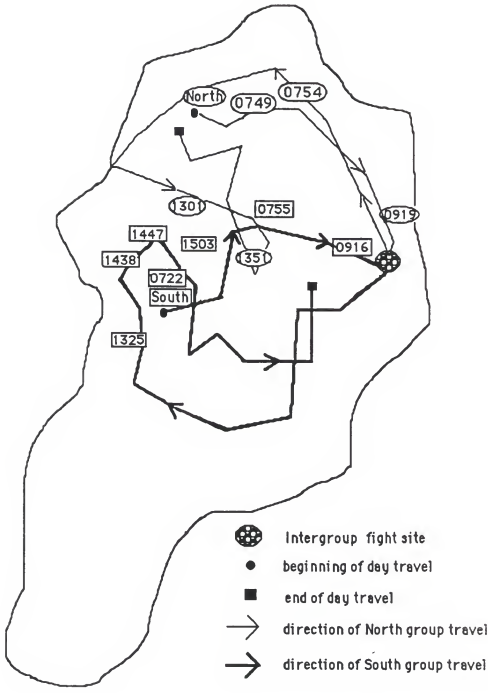
Figure 5.13. Daily travel paths by North and South Mchelelo groups during one day of a month of intergroup fighting. Timing and location of adult male long-calls are plotted for North (ovals) and South (rectangles) groups.


North
1657
1800
1748
0824
0824
0834
1520
1515
1515
0801
0758
0756
South
Intergroup merge site
beginning of day travel
end of day travel
direction of travel North group
direction of travel South group

adult males during merges also was observed; on 4 occasions adult males were observed being aggressive toward sexually receptive females, causing the females to move away from the other group.

Fight months were intermediate to avoid and merge months in range overlap; South group frequently moved through the north sector of the forest and each group occasionally crossed the others' travel path. Vocal responses to long calls were more frequent than during avoid months and calls often resulted in direct, long-distance movements (>150 m) toward the caller (Figure 5.13). When fighting occurred, members of opposing groups lined-up, faced one another and lunged with tails arched forward, heads down, and eye-lids lowered. Occasional, low, "cackling" vocalizations were given by group females. All age-sex classes except infants, participated in fights; adult females participated most in the fighting line-up and only adult males participated in branch-shaking and active chases through the canopy. Intragroup herding by males during fights occurred only once when an adult male forced a group female of unknown receptivity toward a fight. Physical contact during fights was rare; adult females and juvenile males were observed 4 times biting opponents and standing on their back legs battling each other with their front legs. Grooming bouts generally occurred between individuals of the same group after intergroup fights.

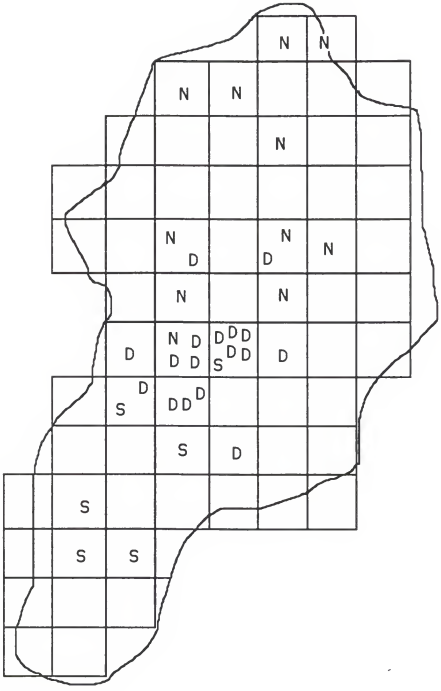
Figure 5.13. Daily travel paths by North and South Mchelelo groups during one day of a month of intergroup fighting. Timing and location of adult male long-calls are plotted for North (ovals) and South (rectangles) groups.


North
0749
0754
1301
0755
0919
1447
1503
1351
0916
1438
0722
South
1325
Intergroup fight site
beginning of day travel
end of day travel
direction of North group travel
direction of South group travel

The outcome of intergroup fights was not determined by group size and was not independent of location. Thirty-four of 40 fights were observed from beginning to end and the winner of 17 fights was determined. The smaller North group (n=18 individuals) supplanted South group (n=28 individuals) in 11 of 17 (65%) fights; South group won the remaining 6 (35%) fights. North group won all fights in the northern sector of the forest and South group won all fights in the southern sector of the forest (Figure 5.14). Of the 17 fights in which no clear winner was identified (both groups withdrew), 14 occurred within a 100 m strip in the middle of the forest. Of the total recorded fights, 63% (n=25) occurred within 25 m of an isolated, seasonally fruiting tree or clusters of fruiting dhoum palms (Hyphaene compressa).

Monthly intergroup behaviors did not affect the frequency of long-calls given by either group males or all calls combined (ANOVA, $p>0.05$); groups called as often during avoid months as they did during either fight or merge months. Group response to long calls, as noted above, appeared to differ among avoid, merge, and fight months. I speculated that response differences were due to the availability and dispersion of fruit resources. I therefore tested for differences in fruit availability and percent time spent eating patchy and uniform foods among the 3 intergroup behavior categories.

Figure 5.14. Location and outcome of 34 fights observed between North and South Mchelelo groups. N and S indicate that North and South group won fights, respectively. D indicates that no clear winner was determined.

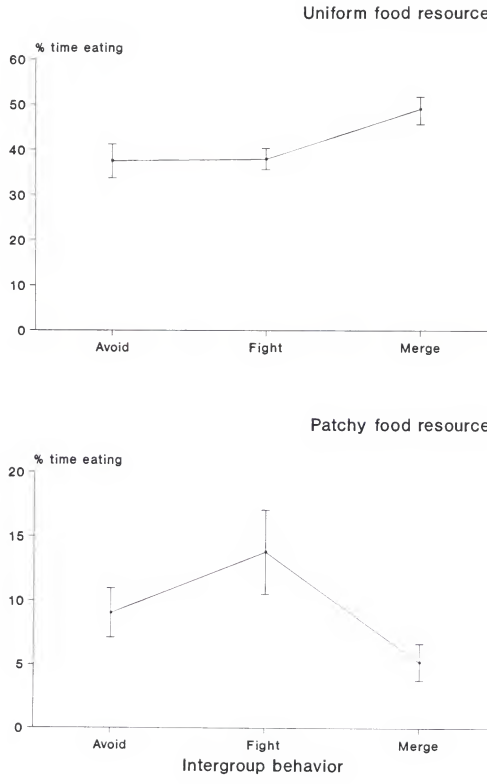

N N
N N
N
N D D N N
N N
D N D D D D D D D D S
S D D D D
S D
S
S S

Total fruit biomass was significantly lower in avoid months ($\bar{x}$=704 kg/ha) than either fight ($\bar{x}$=955 kg/ha) or merge ($\bar{x}$=954 kg/ha) months ($F=10.09$, $df=2,63$, $p<0.0002$). Although total fruit biomass was similar during merge and fights months, the distribution of foods eaten by mangabeys differed. Mangabeys spent significantly more time feeding on uniform food resources during merge months ($F=7.03$, $df=2,59$, $p<0.002$), and significantly more time feeding on patchy food resources during fight months ($F=3.72$, $df=2,59$, $p<0.03$; Figure 5.15).

Discussion

Movements and use of space by Tana mangabeys are influenced by a complex interaction of the spatial and temporal distribution of foods, forest patch size, group size, and intergroup interactions. Results show that fruit availability and distribution influence mangabey use of space but have little effect on movement patterns (backtracking and path length). Because Tana mangabeys occupy small home ranges and cover much of their range in one day, they may be able to continuously monitor fruit production; knowledge of fruit resources would allow them to move directly to areas of high production and reduce the need to search. Robinson (1986) suggested that the lack of consistent correlation between movement patterns and food

Figure 5.15. Percent time North and South Mchelelo groups spent feeding on foods with different distributions as a function of intergroup behavior. a) Percent time feeding on foods with uniform distributions; b) Percent time feeding on foods with a patchy distributions.


Uniform food resources
% time eating
60
50
40
30
20
10
0
Avoid
Fight
Merge
Patchy food resources
% time eating
20
15
10
5
0
Avoid
Fight
Merge
Intergroup behavior

resources of wedge-capped capuchin monkeys (Cebus olivaceus) was due, in part, to their knowledge of resource location and ability to move accordingly.

Invertebrate consumption also did not appear to influence movement patterns. Although invertebrates may be highly renewable, they appeared to be distributed uniformly through the habitat; mangabeys frequently fed on invertebrates in the leaf litter when traveling between fruit trees and no quadrats could be identified as areas of high invertebrate consumption. A uniform distribution of invertebrates would decrease the influence of invertebrate foraging on use of space and movement patterns.

Forest patch size may limit mangabey movements and use of space. Tana mangabeys are constrained in movement by the small size and isolation of the forests they occupy. If groups are unable to travel between neighboring patches, home range and movements are limited as groups reach forest boundaries and are forced to turn or backtrack. Although daily path lengths are similar among Tana mangabeys and other closely related species (Waser 1984), home range estimates for mangabeys occupying larger, less fragmented forests are an order of magnitude greater (Cercocebus galeritus agilis, 200+ ha, Quris 1975; Cercocebus torquatus, 247 ha, Mitani 1989; Cercocebus albigena, 410 ha, Waser 1975). Only the black mangabey (Cercocebus aterrimus) of the Zaire Basin has been reported to have home range sizes

similar to C. g. galeritus (Horn 1987); the study groups however, were unhabituated and the data were not collected systematically. The inconsistency between daily path length and home range size suggests that the Tana mangabey must satisfy requirements similar to other closely related species within a much smaller home range.

Presence of neighboring groups further restricts home range size, use and movement patterns. South Mchelelo group strongly influenced North Mchelelo group's ranging patterns. High rates of backtracking and frequency of long-calls in Nkano forest also indicate that neighboring groups may have restricted Nkano group's movements and home range; despite the larger size of Nkano forest (35 versus 17 ha), the Nkano group's home range was similar in size to North Mchelelo group.

Group size also may affect home range and movements. Waser (1977) showed for Cercocebus albigena that an increase in group size over a certain threshold significantly increased daily path length, and potentially annual home range. South Mchelelo group, the largest of the 3 groups, moved between 2 forests and occupied the largest home range. The relative importance of group size and presence of neighboring groups, however, cannot be determined without additional data on more groups.

Several primate species exhibit facultative territoriality, expressing territoriality only under

particular environmental or social conditions. Butynski (1990), Gartlan and Brain (1968), and Yoshiba (1968) described facultative territoriality for several primate species in response to differing population densities. Others (Hamilton et al. 1976, Kavanagh 1981, Chapman and Fedigan 1984) have documented variable territoriality between species populations in response to differing food resources. Competition for limited resources is essential for the evolution of territoriality, but whether territoriality will evolve is ultimately dependent on the 'economic defendability' of these resources (Brown 1964, Horn 1968). Mitani and Rodman (1979) developed an "index of defendability" (D) based on the frequency with which a group encounters the boundaries of its range; they consider the potential for frequent contacts with range boundaries (range defense) high when $D \geq 1.0$. Indices of defendability for North Mchelelo (D=4.5), South Mchelelo (D=1.5) and Nkano (D=4.5) groups indicate that their home ranges are defendable. Although the conditions for territoriality by mangabeys are present, defense should be expressed only when resources are limited.

My results and those of Homewood's (1976) suggest that seasonal variation in food availability and distribution result in facultative defense of space by Tana mangabeys. When fruit resources are low, or limited, intergroup interactions are rare and groups actively avoid one another.

Neighboring groups often overlap, sharing space and resources but are separate in time (sensu "time-sharing", Jolly 1972). As fruit availability increases, the distribution of plant diet species influences the type of interaction; peaceful, intergroup interactions generally occur when mangabeys eat uniformly distributed species and aggressive interactions occur when mangabeys eat species with patchy distributions.

Similar patterns of intergroup interactions based on resource availability and/or distribution have been demonstrated experimentally for other primate species. Avoidance, mediated through long-range vocalizations, among groups of grey-cheeked mangabeys (Cercocebus albigena) has been demonstrated by Waser (1976). Grey-cheeked mangabeys occupy large (410 ha) home ranges where costs of defense are high relative to potential benefits. Robinson (1985) showed that capuchin monkeys respond to playbacks of spacing vocalizations more aggressively when feeding on patchy food resources than when feeding on more uniformly distributed resources.

Patterns of defense expressed by the Tana mangabey reflect trade-offs between costs and benefits of defending resources of differing distributions. Discrete, isolated resource patches (e.g., fruiting trees) are more easily monopolized than resources with uniform distributions. Benefits accrued through defense of ripe fruit trees also

may be greater than for resources typically showing uniform distributions. A ripe fig for example, offers a locally superabundant source of fleshy fruits high in sugar and low in secondary compounds (Waterman 1984). Fruits of more abundant, uniformly distributed species (e.g., Phoenix reclinata and Diospyros mespiliformes) are eaten primarily unripe and may offer a less easily digested, lower quality reward. Mangabeys also may be less likely to defend uniformly distributed food resources because they impose fewer constraints on available feeding sites and decrease feeding competition. The large, continuous clusters of the palm Phoenix reclinata afford numerous feeding sites for mangabeys and were often sites of peaceful, intergroup interactions. Fruit trees, on the other hand, often could not contain an entire group of mangabeys.

Waser and Homewood (1979) predicted that Tana mangabeys should show tendencies toward defense of space based on their small home ranges, the relatively high productivity of the Tana forests, and the fact that mangabeys often fed on tree species that produce fruit continuously over periods of many months. Field experiments involving long-call playbacks did not support their expectations; Tana mangabeys showed no indication of site-specific territorial defense (Waser and Homewood 1976). My observations however, suggest that response to vocal playbacks (territorial defense) should vary according to resource availability and distribution and

that strong responses are predicted only when food availability is high. Waser and Homewood conducted their experiments during the dry season when measures of food availability were "approximately 1/2 that of the wet season", and a low response, therefore, would be expected. Additional data by Homewood (1976) demonstrated that Tana mangabeys occasionally engaged in aggressive interactions and that peaceful, intergroup interactions occurred primarily during the wet season when fruit resources were high.

The Tana mangabey has been described as an adaptable, generalist species that adjusts to a wide range of environmental conditions (Homewood 1976). Behavioral and dietary flexibility have been shown to buffer seasonal fluctuations in resource availability (Homewood 1978, Chapter 3) and aid in adapting to large-scale habitat change (Chapter 3). The Tana mangabey's flexibility of ranging and intergroup behaviors are additional features of adaptation to a highly seasonal, restricted habitat where food resources fluctuate widely and awareness of neighboring groups is high.

CHAPTER SIX

POPULATION VIABILITY OF THE TANA RIVER CRESTED MANGABEY

Introduction

A major goal in the study of endangered species is to determine the minimum population sizes that can ensure the long-term persistence of the species (Soulé 1980). Although problems exist in the estimation of viable population sizes, there is universal agreement about the importance of such estimates in making informed management decisions (Harris and Allendorf 1989, Soulé 1980).

Genetics and demography offer two very different approaches to the problem of estimating viable populations (Ewens et al. 1987). The genetic approach is concerned with the maintenance of genetic variation and the rate at which this variation is lost through inbreeding or random genetic drift. The demographic approach is concerned with the probability of complete extinction of a population through random demographic events. Although the effects of inbreeding depression and the maintenance of genetic variability have received far more attention than demography in estimating viable population size, researchers have begun to argue that demography may be of more immediate importance than population genetics in determining minimum viable

population sizes (Goodman 1987a, b, Lande 1988, Shaffer and Samson 1985). Population extinction is by definition a demographic process (Lande 1988); the amount of genetic variation within a population becomes irrelevant if a population goes extinct for reasons such as habitat destruction. Demographic characteristics are subject to natural selection and are therefore affected by the genetic composition of a population as well as other factors such as habitat quality and environmental variation (Shaffer 1981, Soulé 1980, Stearns 1976, Goodman 1987b).

Rigid adherence to the results of either approach is potentially dangerous given the confusion over which models produce the best estimates (Harris and Allendorf 1989) and the uncertainties that arise when using limited data bases characteristic of long-lived species studied for very short periods (Dobson and Lyles 1989). Lande (1988) calls for "a realistic integration of demography and population genetics" for examining population viability, although he states that the task of integration has proven formidable and has largely eluded ecologists. Part of the problem is the lack of common variables in genetic and demographic models. A first approach is to perform both analyses and compare the results.

In this chapter, I conduct demographic and genetic analyses separately for the Tana River crested mangabey. Estimates generated from the two approaches are compared and

used to develop a range of viable population sizes. I then evaluate the level of risk facing the mangabey by comparing calculated population sizes with present day population estimates and discuss the potential for achieving such numbers.

Methods

Mangabey Data Set

The number of mangabey groups present in 32 forests where mangabeys are or were known to exist in the mid-1970s was determined during forest surveys conducted in April and May 1989 (Table 6.1). Data for 2 forests surveyed in July 1988 are included with the 1989 data. Comparative data for the mid-1970s were obtained from surveys conducted by Homewood (1976) and Marsh (1976, 1978a).

Data on age and sex composition were collected over 20 months for 3 intensively studied groups and 4 additional groups that were monitored on an opportunistic basis every few months (Table 6.2). Mangabeys form multi-male, female-bonded groups (Homewood 1976). Males disperse as subadults and adult male turnover in groups can be high (Homewood 1976). No data exist as to whether males obtain breeding status more than once in their reproductive lifetime. Observations indicate that the dominant male secures the majority of the copulations (Kinnaird 1990a; but see Homewood 1976) and I assume throughout the calculations that

Table 6.1. Minimum and maximum numbers of mangabey groups censused in forests on the east and west banks of the lower Tana River in 1988-89 and 1973-74. Forests not censused or indicated with (-); those no longer standing indicated with (x). Data from 1973-74 are taken from Homewood (1976) and Marsh (1976, 1978).

East Bank			West Bank		
Forest Name	Year		Forest Name	Year	
	1988-89	1973-74		1988-89	1973-74
Kanjonga	2	2	Guru	2	3-4
Wenje	2	2	Mchelelo	1	2
Maroni	1	1	Sifa	0	1
Guru	1	1	Congolani	0	1
Sifa	2-3	2-3	Congolani C.	2	2
Baomo	1	1	Maridadi	0	1
Marembo	1	1	Baomo N.	1	1-2
Mnazini	2	2-3	Baomo S.	3-4	5-6
Bubesa	0	1	Kitere	1	1
Lemu	-	1	Mnazini/Kano	2	2
Wema 1	1	1	Mnazini	1	2
Home	1	2-3	Woodlands	1	1
Lango la Simba	-	1	Kinyadu	0	1-2
			Bubesa	0	1
Subtotal	14-15	18-19	Matalani	x	1
			Nkame	1	0
			Marembo	1	1-2
			Maziwa	1-2	1-2
			Hewani 1	1	1-2
			Hewani 2	0	1
			Subtotal	18-20	29-39

Totals for both banks 1988-89: 32-35 groups
1973-74: 47-57 groups

Table 6.2. Age-sex composition of 7 mangabey groups with comparative means from 1973-74 (Homewood 1976). AM = adult male (>4-5 yr); SubM = subadult male (3-5 yr); AF = adult female (>4 yr); SubF = subadult female (2.5-3 yr); JM = juvenile male (8 mon-3 yr); JF = juvenile female (8 mon-2.5 yr); IM and IF = infant male and infant female, respectively (≤ 7 mon).

Forest	AM	SubM	AF	SubF	JM	JF	IM**	IF	Total
Mchelelo*	1	0	6	0	5	3	1	1	18
Congolani C*	2	1	6	2	7	6	3	1	28
Kano*	2	0	4	0	3	4	3	1	17
Mnazini	2	0	4	0	3		2		15
Mnazini N 2	2	1	7	0	11		3		24
Guru	2	1	5	0	6		4		18
Baomo N	2	1	8	0	12		2		25
Mean	1.85	0.57	5.85	0.29	8.57		3.00		20.7
1973-74 Mean (n=4 groups)	3.25	3.50	9.75		6.00		2.50		26.5

*main study groups
**4 infants not included died before 6 months of age; 3 were believed to be males, one was not sexed.

the dominant male fathers all infants born in his group during his tenure. Basic reproductive parameters for male and female mangabeys are summarized in Table 6.3.

Population Genetics Model

Effective population size

The first step in developing criteria for minimum population size is determining how much inbreeding, or loss of genetic variability, is acceptable. The quantity of genetic variation in a population is a function of effective population size (N_e), the size of the ideal population that would undergo the same amount of random genetic drift as the actual, or census, population (Wright 1931). To estimate N_e for the mangabey, I used models developed by Lande and Barrowclough (1987). I chose these models because they incorporate the mean and variance of male and female reproductive success, terms that have been shown to be exceedingly important in estimating N_e (Chepko-Sade et al. 1987, Wood 1987, Harris and Allendorf 1989) and avoided the greater number of assumptions necessary for other models (e.g., Hill 1972 and Ryman et al. 1981). Lande and Barrowclough's approach simultaneously incorporates the effects of variance in progeny number (Eq. 1), unequal sex ratio (Eq. 2) and fluctuating population size (Eq. 3):

Equation 1. $N_{em} = (N_m K_m - 1)/[K_m + K_{vm}/K_m) - 1]$ and

$$N_{ef} = (N_f K_f - 1)/[K_f + K_{vf}/K_f) - 1]$$

Table 6.3. Reproductive parameters for male and female mangabeys.*

Parameter	Male	Female
Mean age of first breeding (y)	7	6.5
Maximum recorded lifespan (y)	19	19
Maximum estimated number of reproductive years	12	12.5
Gestation length (d)	--	171
Number of offspring per litter	--	1
Interbirth interval (y)	--	2
Birth season		Aug-Apr

*Sources: Harvey and Clutton-Brock (1987) for C. galeritus spp., Homewood (1976), Kinnaird (1990a), and this study.

where N = number of breeding males or females (denoted by subscript) in the population;

N_e = effective number of males or females (denoted by subscript) in the population;

K = mean number of progeny produced by an individual male or female during its lifetime; and

K_v = variance of K for each sex.

Equation 2. $N_e = 4[(1/N_{em}) + (1/N_{ef})]^{-1}$

Equation 3. $N_e = 1/2\ [1 - (\Pi\ [1 - 1/2N_e(i)]\}^{1/t}]^{-1}$

where $N_e(i)$ = the effective population numbers in different generations; and

t = generation length in years;

Estimating model parameters. Total population size (N) was estimated by multiplying the number of groups within the mangabeys total geographic range (Table 6.1) by the average group size (Table 6.2). N_f and N_m were estimated by multiplying the mean number of breeding females or males per group (Table 6.2) by the total number of groups. Separate calculations were made using minimum and maximum estimates of group numbers and numbers of male and female breeders for both 1973-74 and 1988-89.

Female lifetime reproductive success was simulated for 1000 adult females. Because female mangabeys are capable of producing a maximum of 6.25 infants in their lifetime (Table 6.3), a potential 7 infants were assigned to each of the 1000 females. Assuming a 1:1 sex ratio at birth, sex was

assigned randomly to the infants. Sex-specific probabilities of survival were assigned at random among the 7 infants with values for the 7th infant devalued by 0.75 to account for the probability of a 7th infant not being born. If the generated survival value of any infant was lower than the actual survival rate calculated for each sex from the known group structures (using the ratio of adults to subadults, juveniles and infants, Table 6.2), the infant was considered to have survived. The number of surviving infants was summed for each of the 1000 females; and the mean and variance of female lifetime reproductive success calculated.

A male mangabey's lifetime reproductive success (K_m) is influenced by his ability to secure and retain tenure within a group, the number and reproductive potential of available breeding females, and the survival rate of the offspring (Wade 1979). The probability of a male retaining tenure for at least one year is estimated as:

$p(t) = 1 - (\#\text{ group takeovers}/\#\text{ of breeding male years})$.

Assuming this probability is constant and independent between years, then the probability of retaining tenure for n years is $p(t)^n$. Based on the calculated distribution of $p(t)^n$, I randomly distributed tenure time among 1000 males. Males who retained tenure for less than 9 years after the first run were given the opportunity to secure another group and breed for up to 6 years (approximately 1 generation), such that cumulative tenure was never greater than 12 years.

Those males who had a cumulative tenure of less than 9 years after 2 runs were given a final opportunity to secure a 3rd group for a maximum of 6 years and a total tenure of no more than 12 years. Tenure time was multiplied by the mean number of reproductive females available to a male and the mean number of infants produced annually by a female. Infant production then was devalued by the probability of survival of male and female infants. The mean and variance of infant production by males was calculated for three scenarios: males attain tenure only once in their lifetime; males attain breeding status in a 2nd group after losing tenure in the first; males secure multiple groups (maximum of 3) throughout their reproductive lifetime.

Population subdivision

The effective size of a population will be influenced greatly by the degree of population subdivision. If gene flow between subpopulations, or demes, is so low that they become fixed for alternative alleles, then the effective size of each deme, rather than that of the population as a whole, may need to be considered. Because the Tana mangabey population is distributed among forest patches separated by a major river, limited and non-random gene flow among forests and particularly across the river could create isolated subpopulations. I used a one-dimensional stepping-stone model developed by Kimura and Weiss (1964) and Wright's (1943) island model to determine whether or not

groups within separate forests and on opposite river banks should be considered effectively isolated subpopulations. I chose the one-dimensional stepping stone model instead of a multi-dimensional one (Kimura and Weiss 1964; Slatkin 1985; Wright 1943) to examine gene flow along the river banks because the highly linear arrangement of the forests should limit most gene-flow to adjacent forests. The island model was used to examine gene flow across the river because only 2 subpopulations were considered and migration to distant forests was not possible.

The amount of genetic differentiation between demes is evaluated with a fixation index, F_{st}, the component of genetic variance distributed among demes. F_{st} can vary from 0 to 1; approaching 1 when demes are sufficiently isolated from one another to be fixed for alternative alleles. Although Wright (1978) suggests that F_{st} values as low as 0.05 (equivalent to 5% of the genetic variation being due to differences among groups) may indicate differentiation, other authors give more liberal interpretations of F_{st}, suggesting values ranging from 0.15 to 0.33 would be necessary to indicate great differentiation (Hartl 1980, Allendorf 1983). For the linear stepping-stone model, F_{st} is defined as:

$$F_{st} = 1/(1 + 2N_eC)$$

$$\text{where } C = 2(2m_e * m)^{1/2};$$

m = the fraction of members exchanged with adjacent forests each generation; and

m_e = the fraction of members a forest exchanges with the population as a whole (long distance migration).

When the number of demes, or forests, is finite, the actual expected differentiation is approximated by the product of the above estimate of F_{st} and a correction factor for finite forest number. For a linear case, the correction factor is:

$$[1 - 1/n - (2/n^2)\ (N-i)\ r(i)]$$

where n is the number of demes and

$$r(i) = \exp - (2m_e/m)^{1/2}i$$

Wright's (1943) island model is computed as:

$$F_{st} = 1/(4N_{em} + 1)$$

Estimating model parameters. Little data are available on the dispersal patterns of male mangabeys and indirect estimates of numbers of migrants (M) must be used. One estimate of M is the potential number of males produced by a deme in one generation that could migrate to a neighboring deme and breed. Given a 1:1 sex ratio at birth, this is calculated as:

$$M = [(t)(A_f)(R_f)/2](S_m)$$

where t = generation length in years

A_f = average number of reproductive females/group

R_f = average female reproduction/year

S_m = probability of an infant male surviving to reproduce.

The estimated fraction of members exchanged with adjacent forests each generation (m) is simply M/N, where N is the number of breeders present in a given deme (Allendorf 1983). The rate of long-distance migration (m_∞) is taken to be of the same order as mutation, i.e. 10^{-4} (Kimura and Weiss 1964, Lande and Barrowclough 1987).

Demographic Extinction Model

I chose a demographic extinction model developed by Goodman (1987b) and approximated by Belovsky (1987) that calculates average persistence time for a population of a given size with certain demographic parameters:

$$T = [(N-1)V - r][(V+r/V-r)(1/r(V-r)(\sum_{y=1}^{N} 1/y^2) - 1/r(\sum_{y=1}^{N} 1/y(yV-r)) - 2V/V-r(\sum_{y=1}^{N} 1/y^2)(\sum_{y=1}^{N} 1/[(y-1)V - r](yV-r)]$$

where T = expected persistence time;

r = mean per-capita population growth rate;

V = variance of r attributed to environmental fluctuations;

N = maximum population size

Estimating model parameters. Per-capita population growth rate (r) was calculated for the 3 main study groups

using the observed exponential rate of increase. Per-capita growth rates for the 3 groups were averaged and a variance calculated. Because the 3 study groups occupied very different forest habitats, I assumed environmental variation between them to be independent and that the variance was characteristic of the population as a whole. I also assumed that each group sampled sufficient individuals such that the contribution of independent variation between individuals would be negligible relative to that attributed to the environment. I calculated a second estimate of r for comparison following Cole's (1954) method.

I followed Belovsky's (1987) recommendations for estimating V by first computing the ratio of variance in r to mean r in the absence of environmental variation:

$$(2b/r) - 1$$

where b = birth rate and

r = mean per-capita growth rate.

This ratio is multiplied by the square of the coefficient of variation of r for the 3 study groups to obtain an estimate of the ratio between r's variance due to the environment and mean r. The final estimate of V is obtained by multiplying by mean r.

Results

Estimates of N.

Parameter values and estimates of effective population size for Eq. 1 and 2 of Lande and Barrowclough's model are

computed for 2 time periods, 15 years apart, or approximately 2 mangabey generations (Table 6.4). Minimum and maximum population estimates (N) reflect the population decline over the 15-year period. Values of N_m and N_f for the 2 periods indicate little change in the breeding sex ratio. Because males had a greater number of breeding females available in 1973-74, separate estimates of lifetime reproductive success were calculated for the 2 periods (Figures 6.1 and 6.2). Male reproductive success is illustrated for 1973-74 and 1988-89 for three simulations where a male attains tenure once, twice or three times during his reproductive lifespan. Both the mean and variance of male reproductive success increased when a male was given the opportunity to secure breeding status in a 2nd and 3rd group. Relative to the mean however, variance decreased with increasing reproductive success. Variance in progeny number for males is higher than for females in all situations, as would be expected for polygamous species (Wade and Arnold 1980), and always exceeds the mean. Variance in female infant production however, was lower than the mean and resulted in effective numbers of females (N_{ef}) being slightly greater than the census numbers (N_f).

Using Eq. 3 for fluctuating population size, I arrive at a final range of effective population sizes of 87 to 135 mangabeys. This range of estimates does not incorporate the effects of overlapping generations. Models for overlapping

Table 6.4. Minimum and maximum parameter values and estimates of effective population size for differing numbers of male tenure. N = census number of males or females; K = estimate of lifetime reproductive success of males or females; K_v = variance in lifetime reproductive success; and N_e = effective population size. Subscripts denote parameters for males vs females.

	1973-74		1988-89	
Parameter	Min	Max	Min	Max
N	1245	1511	683	725
N_m	47	57	32	35
N_f	458	556	193	205
K_f	2.57	2.57	2.57	2.57
K_{vf}	1.84	1.84	1.84	1.84
N_{ef}	514	624	216	230
1 male tenure				
K_m	7.41	7.41	4.45	4.45
K_{vm}	44.13	44.13	15.88	15.88
N_{em}	28	34	20	22
N_e	107	129	74	80
2 male tenures				
K_m	11.85	11.8	7.13	7.13
K_{vm}	56.37	56.37	20.41	20.41
N_{em}	36	43	26	28
N_e	133	162	93	99
3 male tenures				
K_m	15.75	15.75	9.47	9.47
K_{vm}	60.32	60.32	21.82	21.82
N_{em}	40	48	28	31
N_e	148	179	99	108

Figure 6.1. Distribution of estimated female lifetime reproductive success. Infant values are rounded to the nearest whole number.

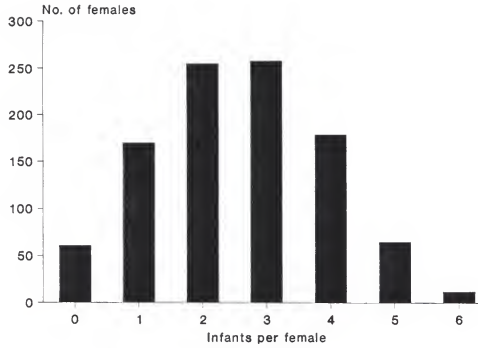
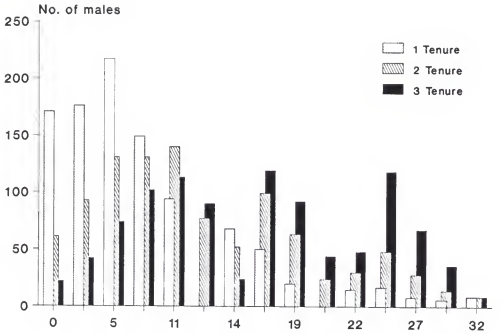
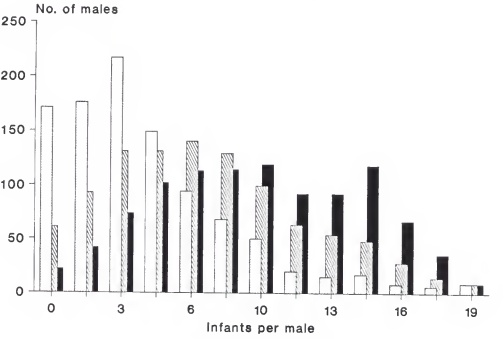

No. of females
300
250
200
150
100
50
0
0
1
2
3
4
5
6
Infants per female

Figure 6.2. Distribution of male lifetime reproductive success estimated for males with 1, 2 and 3 tenures as a dominant, breeding group male. a) 1973-74 male lifetime reproductive success calculated for 1 male:9.75 females; b) 1988-89 male lifetime reproductive success calculated for 1 male:5.85 females.

1973-74
(1 Male:9.75 Females)



1988-89
(1 Male:5.85 Females)



generations require detailed life-tables which are not available for the mangabey. Without incorporating the effects of overlapping generations, the final estimates will be overestimates, probably by a factor of 2 (Soulé 1980).

Population Subdivision

Values for genetic fixation between demes (F_{st}) based on estimated levels of migration (Table 6.5), indicate that forest demes along either bank of the river are not effectively isolated from one another. Over 95% of the genetic variance within the population may be due to differences within the forests and only 4%-5% of the genetic variance (F_{st} East=0.036, F_{st} West = 0.048) appears to be due to differentiation among the forests. Because estimates of m (Table 6.5) do not incorporate secondary transfer by males, the reported F_{st} values likely overestimate the amount of differentiation and therefore are conservative. Estimates of m used, however, are not unrealistic when m is viewed as an emigration rate that is influenced more by the number of potential breeding slots available in a neighboring deme within 1 generation than by the actual number of migrants leaving a deme. With an estimated mean male tenure time of approximately 3 years, 2 males every 6 years (equivalent to 2 males/generation) could on average gain access to a neighboring deme and breed. Considering each deme in a linear array has 2 neighbors, a maximum number of 4

Table 6.5. Parameter values and estimates of the genetic fixation index, F_{st}, for forests on the east and west banks and for west bank and east bank subpopulations. East vs west bank figures are calculated for group migration from one bank to the other for two estimates of high flood frequency.

Number of forests	Mean N_e/ forest	m	m	Fst
10 (East Bank)	3.19	.522	.00004	.036
13 (West Bank)	3.02	.516	.00004	.048
2 (East and West Bank)				
80 year floods	35.9	.005*	-	.579
50 year floods	35.9	.007*	-	.495

*migration rates adjusted to account for an average of 6.85 breeding individuals (males and females) transferring instead of males alone.

migrants/generation (m=0.58) could potentially gain access to a group and breed.

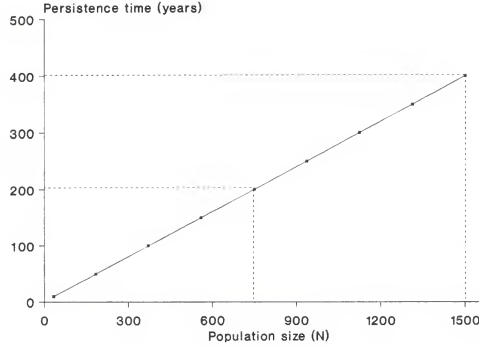
The Tana River may form a major impediment to gene flow. This is indicated by the high F_{st} values calculated when considering combined forest demes on opposite river banks as 2 subpopulations. Gene flow across the river occurs during times of major flooding when breaks in river meanders result in whole forests and their groups shifting from one side of the river to the other. F_{st} values were high whether major floods were assumed to occur on average every 1 in 80 years (Dunne and Leopold 1978) (F_{st} = 0.579) or every 1 in 50 years (Kenya Ministry of Water Development 1978) (F_{st} = 0.492).

Demographic Extinction Model

Estimates of r calculated from population growth (r=0.110) and the Cole equation (r=0.108) were similar. I therefore considered 0.110 an adequate estimate of r for the extinction model. V was estimated at 0.20058, a value close to Goodman's (1987b) assumption that V>2r.

I computed the relationship between T and a range of N's that incorporated maximum population estimates for mangabeys during 1973-74 and 1988-89 (Figure 6.3). In 15 years (1974-1989), minimum estimated population size declined from approximately 1,500 to 725 individuals and mean anticipated population persistence times correspondingly declined from 425 to less than 200 years. A

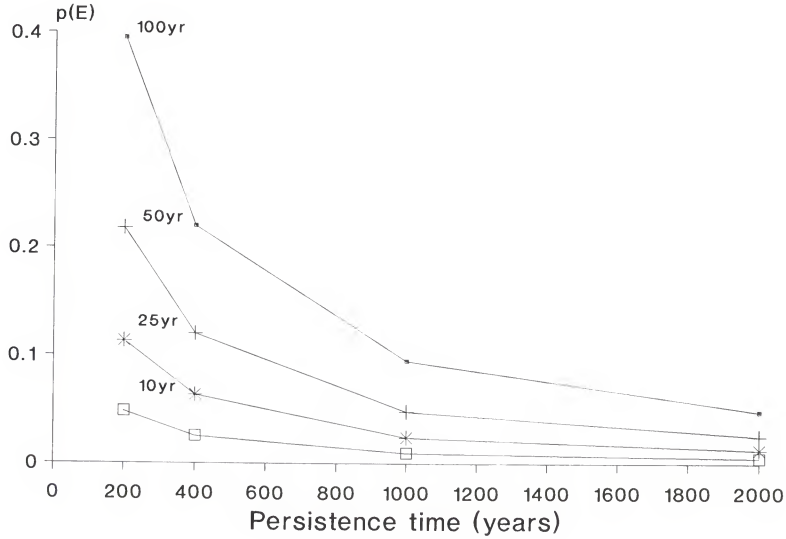
Figure 6.3. Persistence time in years as a function of population size (N). Dashed lines connect 1973-74 and 1988-89 population sizes to estimated mean persistence times.


Persistence time (years)
500
400
300
200
100
0
0
300
600
900
1200
1500
Population size (N)

population of 725 individuals however, will not necessarily survive over the next 200 years. Expected persistence time is distributed as a negative exponential; for a population of a given size with a large expected persistence time, a majority of populations of that size will persist for less time and a few will persist for more time. To achieve a given persistence time with a high degree of certainty (e.g. 95%), the average persistence time will need to be much greater.

I generated distributions of persistence times to determine probabilities of extinction within a given time period for mean persistence times of 200, 400, 1000 and 2000 years (Figure 6.4). For each mean persistence time, 10 samples of 1000 values were randomly generated using a negative exponential distribution. For each sample, the proportion of persistence times less than 100, 50, 25 and 10 years respectively, were computed. These proportions were averaged over the 10 samples and the averages were used as the probabilities of going extinct within a given time period. The results show that for a mean persistence time of 200, the probability of extinction over the next 100 years is approximately 40%. Shorter extinction intervals have higher probabilities of persistence but it is not until the very short-term extinction interval of 10 years that there is a 95% probability of the population persisting. To assure a 95% probability of population persistence over the next

Figure 6.4. Probability of extinction p(E) within 100, 50, 25 and 10 years (denoted by labeled curves) for populations with mean persistence times (T) of 200 to 2000 years.


p(E)
0.4
0.3
0.2
0.1
0
100yr
50yr
25yr
10yr
0
200
400
600
800
1000
1200
1400
1600
1800
2000
Persistence time (years)

100 years, a mean persistence time of 2000 years, or a population of nearly 8000 individuals, is necessary.

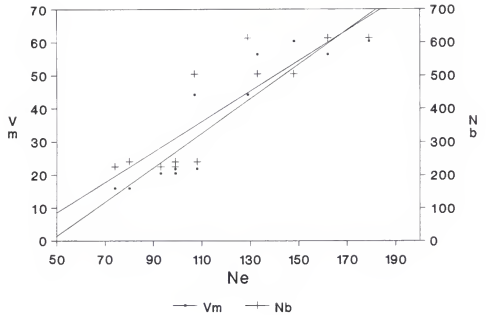
Discussion

Effective Population Size

Estimates of effective population size for the Tana mangabey varied widely (up to 64%) as a function of the initial size of the breeder population and the values used for male lifetime reproductive success. Chepko-Sade et al. (1987) state that for mammals, reproductive variance has the greatest effect on N_e; N_e declines with increasing reproductive variance. This is true, however, only when mean reproductive success is constant. For the mangabey, the initial number of breeders had as great an effect on N_e as the variance in male reproductive success (Figure 6.5). N_e increased with increasing male variance in progeny production. As male mangabeys were given more opportunities to breed by increasing numbers of tenures, mean male reproductive success increased with the variance. Thus, it is the ratio of the mean to the variance that appears to be influencing N_e for mangabeys rather than variance alone. This may be true for primates in general or populations of other long-lived, polygamous mammals.

The least conservative estimates of N_e (from 99-108) suggest that the Tana mangabey is at risk of losing genetic variation. Values of N_e calculated with the highest

Figure 6.5. Effective population size (N_e) as a function of number of breeders (N_b) and variance of male lifetime reproductive success (V_m).


70
60
50
40
30
20
10
0
Vm
700
600
500
400
300
200
100
0
Nb
50
70
90
110
130
150
170
190
Ne
Vm
Nb

parameter estimates of breeder population size and male and female lifetime reproductive success, are far below Lande and Barrowclough's (1987) suggested effective population size of >500 for maintenance of quantitative variance under stabilizing or neutral selection. That groups on opposite banks of the river are effectively isolated does not improve the situation and suggests that the effective population size of concern may be that for the separate river bank subpopulations. Effective population sizes for the east and west bank demes average around 36 individuals; such small subpopulations may not protect against the loss of the majority of genetic variation (Soulé 1980).

Harris and Allendorf (1989) state that "for management purposes, it is probably unnecessary to strive for great precision in N_e estimates. Given the likely uncertainties in data necessary for its calculation by any method, excessively rigid dependence on even the best of estimations is unwarranted". My data result from a relatively short-term study of a long-lived species, therefore much of the demographic data are limited in quality and consequently there are uncertainties in the parameter estimates. The N_e's reported here should nevertheless reflect the best estimates of effective population size of the Tana mangabey and provide good first approximations of the potential magnitude of the problem and the range of genetic loss likely to take place.

Demographic Extinction Model

The results of my data applied to Goodman's (1987b) model suggest that Tana mangabeys have a high probability of extinction within the next 50-100 years given their present population status. The model required very high population numbers for long-term persistence; a population of 8000 mangabeys was necessary to ensure a 95% probability of survival over the next 100 years. The Tana mangabey population, however, could not presently attain, and very likely never has attained such high numbers, given its limited range. Goodman (1987a) found that his model often predicts impossibly large numbers for long-term persistence. He suggests that rare species may persist in spite of predictions because they may not be governed by dynamics with strong environmental variance like those developed in his demographic model. The Tana mangabey is a highly adaptable, generalist species within it's habitat (Homewood 1976). It may be capable for example, of major dietary shifts in response to habitat change (Chapter 3) and therefore may be less sensitive to environmental variance.

Population sizes predicted by Goodman's model were not unrealistically high for the mangabey when lower probabilities of long-term persistence were considered. If an 80% probability of survival over the next 100 years is an acceptable management objective, then a mean persistence time of around 400 years with a corresponding population of

2000 individuals would be adequate. This estimate is still 3 times greater than the present mangabey population size but close to the population sizes reported for mangabeys in the mid 1970s.

Models incorporating details of a species life history and demography often require larger populations than those based on genetic grounds alone (Lande 1988). Application of data for the Tana mangabey to both genetic and demographic models result in very similar population requirements. Given the relationship between current population sizes and calculated N_e's (N_e/N), a census population of 3600-4500 individuals would be required if an N_e of 500 is considered necessary to maintain genetic variability within the population. If the effect of isolation between river banks is considered, as many as 9000 mangabeys may be necessary to achieve an N_e of 500. These requirements are very similar to those predicted by the demographic model for a 95% probability of persistence over the next 100 years. Although these similarities may be fortuitous, the important point is that two very different approaches to population viability indicate that the mangabey is at risk at its present population size and require populations of the same order of magnitude to avert loss of genetic variance or probable extinction.

One of the most important results of viability analysis to date is that viable populations generally are large, so

large that it often will be impossible to contain the required number of individuals in reserves and sanctuaries (Soulé 1987). This is particularly true for the Tana mangabey with a distribution along approximately 60 km of floodplain forest, less than 1/3 of which is protected within the Tana River National Primate Reserve. It would be an unrealistic management goal to strive for population numbers as great as those required by the models given the arguments made above and the mangabeys' severe habitat constraints. The projections allow us, however, to compare ideal population sizes to real populations and to use the results as a guide to determine future actions necessary for conservation.

In the case of the Tana mangabey, the results of the models do not give an optimistic picture; Tana mangabeys may not survive without drastic management measures. Because the mangabey is a generalist species that easily exploits new habitats (Homewood 1976), it should respond well to habitat management. The fact that the framework for such management exists within the Tana River National Primate Reserve gives cause for hope.

CHAPTER SEVEN

CONCLUSION

This study has demonstrated the flexibility of Tana mangabey activity patterns and feeding, ranging, and intergroup behaviors in response to seasonal and large-scale habitat changes. Mangabeys adjust activity patterns not only to buffer fluctuations in resource availability in a highly seasonal habitat, but to compensate for permanent loss of habitat and critical food resources. As resources decline in availability, mangabeys spend more time feeding and less time inactive or engaged in social grooming. Mangabeys are opportunistic feeders; they have a relatively diverse diet but concentrate on what is most available at any given time and are capable of responding to habitat alterations through major dietary shifts. A decline in numbers of important diet trees over the last 15 years appears to have caused mangabeys to shift from primarily ripe, fleshy fruits to unripe seeds and insects.

The Tana mangabey's flexibility of ranging and intergroup behaviors are additional features of adaptation to a highly seasonal and restricted habitat. My results suggest that seasonal variation in food availability and

distribution result in facultative defense of space by Tana mangabeys. As fruit availability increases, the distribution of plant species in the diet influences the type of interaction; peaceful, intergroup interactions generally occur when mangabeys eat evenly distributed species and aggressive interactions occur when mangabeys eat species with patchy distributions. The question of whether defense has increased over the last 15 years as fruit resources became more limiting and distributions changed could not be adequately addressed with the available database and poses interesting questions for future work.

The flexible behavioral attributes of the Tana mangabey make it well suited for highly dynamic, naturally patchy riverine forests. There are, however, limitations to the adaptability of any species; the Tana mangabey is limited by habitat quality and other specific requirements. My results show that mangabey groups go extinct as forests become isolated from the river and senescence. Small forests, isolated from neighboring patches, support fewer mangabey groups than larger, less isolated forests (Kinnaird unpubl. data). The presence of particular food species also may be critical to mangabey presence and/or persistence in a forest. For example, Phoenix reclinata and Ficus spp. provide critical resources when other fruits are unavailable and may greatly improve patch quality for mangabeys. Mangabey population size therefore is limited by the number

of suitable forest patches. Demographic and genetic models of population persistence indicate that the present population size may not be adequate to avert loss of genetic variability or probable extinction. Low dispersal rates between isolated forest patches or groups on opposite banks of the river also may pose additional problems for the long-term persistence of the population.

If the Tana mangabey is to persist over the next 80-100 years, an increase in suitable habitat will be necessary. Presently, however, forest area is decreasing, and the remaining forest is becoming more fragmented (personal observation). These processes are attributed, in part, to changes in the rivers course and patterns of flooding. Selective felling of trees and forest clearing for agriculture, however, are more immediate and perhaps more pervasive causes of habitat degradation and loss.

The extraction of canopy trees for canoes and beehives, the cutting of trees for building poles, or the intensive use of palm fronds for roofing and weaving material result in the loss of trees important in the mangabey's diet and, in the case of palms, reduced fruit production. Low and unpredictable crop yields and human population growth encourage forest removal to maintain adequate agricultural production. Loss of forest area, for whatever cause, is not balanced by regeneration of new forest (Hughes 1985); forests are being lost faster than they are regenerating.

The best remaining habitat outside the reserve (Wema/Hewani) is being seriously affected by the development of the Tana Delta Rice Irrigation Scheme (Medley et al. 1989); forests have been eliminated or fragmented, selectively harvested, burned, and exposed to entirely different flooding regimes depending on where they occur in relation to the irrigation dikes. Kinnaird (1990b) speculated that mangabey groups living in these forests were critical for improving mangabey population viability by increasing overall population size and supplying additional pools of potentially successful immigrants. The degradation of Wema/Hewani forest area underscores the importance of the remaining forests of the TRNPR.

Clearly, the situation is critical. Immediate action towards habitat preservation and enhancement of existing forest area will be necessary for the conservation of the Tana River crested mangabey and its riverine forest habitat. Kinnaird et al. (1990) have developed management recommendations for the TRNPR that are hoped to form the basis of a government action plan. The recommendations center on preservation of existing habitat through prevention of further forest clearing and taking of forest products. Resettlement assistance for agriculturalists living or farming within the reserve and establishment of alternate sources of tree products such as subsidized aluminum canoes and woodlots for propagating building poles

and palms are necessary elements of an action plan. The second theme central to the recommendations is habitat improvement. The establishment of habitat corridors between forests by planting trees and encouraging natural regeneration is strongly recommended; corridors effectively create larger forest areas and encourage movement and gene flow between isolated primate groups. Increasing forest area within suitable habitat and enriching existing forests by tree planting and protection against fire are important measures for forest areas with primate groups that are far removed from other forests, and may allow or encourage recolonization of small forests that have lost all primate groups.

Manipulation of mangabey groups is another management consideration. Although translocation of mangabey groups from "doomed forests" and adult male mangabeys between river banks should decrease loss of groups and improve gene flow, several problems must be considered: a) the logistics of translocating endangered species are not trivial; b) the probabilities of new males securing groups are not known and may be low; and c) group take-overs may be associated with infanticide (Kinnaird 1990a), thereby lowering infant survival rates.

Kinnaird et al. (1990) state that "the unique biological attributes of the TRNPR combined with its highly threatened status, warrant national park status". National park status

coupled with incorporation of surrounding villages into a buffer zone could improve regional conservation and benefit villagers from activities directly and indirectly related to the park (e.g. tourism). Recent, growing concern by the Kenyan government and its Wildlife Service for the TRNPR, and their possible implementation of the above management recommendations gives cause for optimism for the future of the reserve and its endangered primates.

APPENDIX A

ESTIMATING TREE CANOPY SURFACE AREA AND VOLUME

Tree canopies display an abundance of shapes, varying from the classic "Christmas tree" form to the flat, spreading, umbrella shape of an Acacia. Some tree canopies approximate geometric forms such as cones or spheres but many others, exhibiting odd shapes and canopy irregularites, do not. Deciding on geometric formulae when estimating the surface area and volume of tree canopies therefore is problematic. To determine a geometric form that could best generalized across various shapes, I generated a set of dimensions and calculated surface area and volume based on formulae for different geometric shapes. I then correlated the areas and volumes generated from all formulae. The shape giving areas and volumes that correlated best with all others was considered the most generalizable.

Values varying from 1-3 were used for 3 dimensions: height, radius 1 and radius 2. All possible combinations for the 3 dimensions were made, giving a total sample of 27 sets of dimensions, or tree shapes. I calculated surface area and volumes for all sets using formulas for 6 geometric shapes: 1) an open-bottomed cylinder, 2) a cone, 3) a 1/2 sphere, 4) the zone of a spheriod, 5) a 1/2 oblate spheroid and 6) a

1/2 prolate spheroid (for formulas see CRC Standard Mathematical Tables 1970). I also tested 2 canopy indices developed by Struhsaker (1976) and Marsh (1978a) that make few assumptions about tree shape. The Struhsaker and Marsh indices are calculated as the sum and the product, respectively, of tree depth and tree width.

The descriptive statistics and simple correlations for the area and volume calculations are as follows:

	Surface Area			Volume			N
Formula	Mean (S.D.)	Minimum	Maximum	Mean (S.D.)	Minimum	Maximum	
Cylinder	38.7 (18.4)	9.4	84.8	27.2 (19.8)	3.1	84.8	27
Cone	32.7 (16.0)	7.6	68.3	9.1 (6.6)	1.0	28.3	27
1/2 Sphere	27.2 (14.9)	6.3	56.6	21.0 (16.4)	2.1	56.6	27
Sphere Zone	28.3 (12.9)	6.3	56.6	39.8 (28.0)	4.2	113.1	27
1/2 Oblate Spheriod	24.7 (10.9)	11.1	44.5	20.0 (14.7)	2.1	56.6	11
1/2 Prolate Spheriod	27.3 (11.7)	10.7	44.6	13.2 (13.9)	2.1	56.6	11
Struhsaker	4.0 (1.0)	2.0	6.0	4.0 (1.0)	2.0	6.0	27
Marsh	4.0 (2.1)	1.0	9.0	4.0 (2.1)	1.0	9.0	27

Surface Area Correlations:

	Cone	Sphere	1/2 Sphere Zone	Oblate	1/2 Prolate	1/2 Struhsaker	Cylinder
Cylinder							
Cone	0.91						
1/2 Sphere	0.80	0.98					
Sphere Zone	0.92	0.74	0.58				
1/2 Oblate	0.99	0.96	0.93	0.92			
1/2 Prolate	0.99	0.99	0.97	0.99			
Struhsaker	0.92	0.73	0.57	0.97	0.98	0.95	
Marsh	0.94	0.72	0.55	1.00	0.92	0.99	0.97

Volume Correlations:

	Cylinder	Cone	1/2 Sphere	Sphere Zone	1/2 Oblate	1/2 Prolate	Struhsaker
Cylinder							
Cone	1.00						
1/2 Sphere	0.75	0.75					
Sphere Zone	0.94	0.94	0.52				
1/2 Oblate	1.00	1.00	0.97	0.95			
1/2 Prolate	0.95	0.95	0.61	0.98			
Struhsaker	0.90	0.90	0.55	0.96	0.89	0.89	
Marsh	0.95	0.95	0.53	0.98	0.98	0.98	0.97

All geometric shapes are highly correlated, however, the open-bottom cylinder is the most highly and consistently

correlated with all other shapes for both the surface area and volume calculations. I therefore chose to use the cylinder formula to approximate surface area and volume (i.e. food-producing area) of trees of differing shapes. Although this formula will not give the true values for any given tree due to variation in overall shape and canopy peculiarities, it should be the most applicable and give the best approximation. Using a geometric formula such as the open-bottom cylinder also avoids the problems of linear indices such as those of Struhsaker and Marsh. These indices frequently result in ties even when there are large crown differences. If tree canopies are being ranked, these indices will not be able to distinguish what may be large differences in canopy surface area and volume.

APPENDIX B

NUMBER OF FEEDING RECORDS AND PERCENT OF TOTAL RECORDS BY PLANT TAXON AND MANGABEY GROUP

Taxon	N. Mchelelo		S. Mchelelo		Nkano	
	No. of records	%	No. of records	%	No. of records	%
ALANGIACEAE						
Alangium salviifolium	87	3.3	75	4.4	78	4.1
ANACARDIACEAE						
Lannea schweinfurthii	73	2.4	-	-	-	-
Sorindeia madagascariensis	49	1.6	44	2.6	-	-
APOCYNACEAE						
Hunteria zeylanica	22	0.7	2	0.1	-	-
Rauvolfia mombasiana	40	1.3	-	-	-	-
Saba comorensis	55	1.8	41	2.4	377	19.7
ARACEAE						
Philodendron sp.	-	-	-	-	1	0.05
BORAGINACEAE						
Cordia goetzei	9	0.3	-	-	3	0.2
CAESALPINIACEAE						
Cynometra lukei	22	1.0	-	-	-	-
COMMELINIACEAE						
Commelina sp.	4	0.1	-	-	2	0.1
COMPOSITAE						
Pluchea dioscoridis	-	-	1	0.06	-	-
CUCURBITACEAE						
Coccinia grandis	1	0.03	17	1.0	4	0.2
Kedrostis foetidissima	12	0.4	11	0.7	-	-
EBENACEAE						
Diospyros ferrea	15	0.5	-	-	-	-
Diospyros mespiliformes	114	3.6	85	5.0	14	0.7

APPENDIX B -- Continued

Taxon	N. Mchelelo		S. Mchelelo		Nkano	
	No. of records	%	No. of records	%	No. of records	%
EUPHORBIACEAE						
Antidesma venosum	19	0.6	4	0.2	2	0.1
Drypetes natalensis	1	0.03	2	0.1	5	0.3
FLACOURTIACEAE						
Oncoba spinosa	251	8.1	69	4.0	13	0.7
GRAMINEAE						
grasses (including Urochloa setigera)	75	2.5	85	5.0	54	2.8
GUTTIFERAE						
Garcinia livingstonei	10	0.3	21	1.2	4	0.2
MALVACEAE						
Abutilon mauritianum	12	0.4	-	-	-	-
Hibiscus micranthus	-	-	-	-	1	0.05
Thespesia danis	-	-	2	0.1	-	-
MIMOSACEAE						
Acacia robusta	104	3.2	6	0.4	1	0.05
Albizia gummifera	16	0.5	4	0.2	-	-
MORACEAE						
Ficus bubu	14	0.5	-	-	1	0.05
Ficus bussei	-	-	43	2.5	-	-
MORACEAE						
Ficus natalensis	128	4.1	63	3.7	-	-
Ficus sycomorus	90	2.9	43	2.5	342	17.9
PALMAE						
Borassus aethiopium	-	-	1	0.06	1	0.05
Hyphaene compressa	322	10.4	137	8.0	-	-
Phoenix reclinata	1012	32.7	602	35.2	449	23.3
PAPILIONACEAE						
Rhynchosia viscosa	2	0.07	-	-	1	0.05
SALICACEAE						
Populus illicifolia	-	-	1	0.06	-	-

APPENDIX B. -- Continued

Taxon	N. Mchelelo		S. Mchelelo		Nkano	
	No. of records	%	No. of records	%	No. of records	%
SAPINDACEAE						
Aporrhiza paniculata	140	4.5	94	5.5	233	12.2
Blighia unijugata	-	-	-	-	1	0.05
Chythranthus obliquinervis	-	-	-	-	2	0.1
Majidea zanguebarica	-	-	1	0.06	-	-
Tamarindus indica	97	3.1	22	1.3	-	-
SAPOTACEAE						
Mimusops fruitcosa	41	1.3	74	4.3	-	-
Pachystela msolo	19	0.6	2	0.1	219	11.4
SIMAROUBACEAE						
Harrisonia abyssinica	16	0.5	-	-	-	-
STERCULIACEAE						
Sterculia rhynchocarpa	-	-	-	-	5	0.6
RUBIACEAE						
Rubiaceae sp.	1	0.03	10	0.6	-	-
Pavetta sphaerobotrys	8	0.3	6	0.4	1	0.05
Polysphaeria multiflora	21	0.7	10	0.6	63	3.3
URTICACEAE						
stinging nettle	22	0.7	8	0.5	-	-
VITACEAE						
Cissus rotundifolia	23	0.7	16	0.9	6	0.3
Cyphostemma jiquu	2	0.07	-	-	-	-
VIOLACEAE						
Rinorea elliptica	-	-	-	-	9	0.5
CODED TAXA						
vine 1	10	0.3	4	0.2	-	-
vine 2	1	0.03	-	-	-	-
vine 3	-	-	-	-	8	0.4
Mwimbo vine	5	0.03	-	-	-	-
Code MK1	-	-	-	-	3	0.2
Code ALE	1	0.03	-	-	-	-
mushrooms (all spp.)	104	3.3	72	4.2	13	0.7
Total	3070		1678		1916	

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BIOGRAPHICAL SKETCH

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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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